PARENTAL CARE AND SEXUAL SELECTION IN SOCIALLY MONOGAMOUS CRESTED AUKLETS (AETHIA CRISTATELLA)

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PARENTAL CARE AND SEXUAL SELECTION IN SOCIALLY MONOGAMOUS CRESTED AUKLETS (*AETHIA CRISTATELLA*)

by

Gail S. Fraser

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ABSTRACT

In this thesis I investigate the relationships between chick growth, parental attendance and sexual selection in a seabird that exhibits mutual mate choice. I quantified breeding parameters, sexual roles in parental care and how ornamentation relates to parental care in Crested Auklets (*Aethia cristatella*) at Buldir Island, Alaska. Growth rates averaged about 9.98 g/day during the linear phase and chicks fledged at an average mass of 247 g and a wing length of 124 mm at 34.5 days after hatching. Crested Auklet chicks, like those of other diurnally active auklet species, grow relatively fast and depart at a younger age compared to the chicks of two nocturnal auklet species. Parental care patterns were studied using radio telemetry. In 1996, I found no sexual differences in parental care behaviours and low attendance rates, suggesting a poor food year. In 1997 and 1998, I found significant differences in parental care between males and females: males attended and brooded their single chick 45% more than females, while females provisioned 47% more than males. Males have a larger and strongly hooked bill and are more aggressive than females and I hypothesized that males are better equipped than females to guard young chicks. While this bill shape difference probably evolved through intra-sexual selection, it has ecological consequences because male auklets delivered larger prey items than females. Males brought in 30% more larger euphausiids whereas females brought in 36% more smaller copepods. I examined the relationship between crest length and parental effort using simple game theory models. I evaluated whether crest length indicated an ability

to provide parental care (a direct benefit) or whether crest length advertised a indirect benefit such as good genes. Male attendance and provisioning rates were not related to crest length, however early chick provisioning by males was positively correlated with their partner's crest length. Female provisioning rates were negatively correlated with own crest length, while early attendance was positively correlated with their partner's crest length. Because both male and female parental effort was positively correlated with their partner's crest length, suggests that crest length was an advertisement of an indirect benefit.

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INTRODUCTION AND OVERVIEW

Seabirds present a remarkable opportunity to study life history strategies because they are long-lived, have low reproductive rates and usually live on isolated islands in colonies, but allow the researcher to quantify the behaviour and reproductive success at one location (Lack 1968). Seabirds must overcome a number of obstacles in order to successfully reproduce in an environment that has ephemeral and patchy prey that is often far from the colony. Auks in particular, are unique in that they are the only family to have evolved a wide variety of reproductive and chick development strategies adapted to their marine environment (Gaston and Jones 1998). Ancient Murrelets (*Synthliboramphus antiquus)* represent one end of the extreme with their tiny precocial chicks fledging to sea at two days old, while puffins (*Fratercula* spp.) at the other end with their one chick staying at the nest site for 70 days or more fledging close to adult size. Murres (*Uria* spp.) and Razorbills (*Alca torda*) are considered 'intermediates' because their one chick fledges from the nest site well before achieving adult size. Auklets, (genus *Aethia*) while similar to puffins in that they have semi-precocial chicks that fledge close to adult size, are different in that their chicks grow more quickly (Gaston and Jones 1998). The processes driving such a large amount of variation of reproductive strategies among the different auk species in chick development are still open for debate and the more information we acquire on each species the better our understanding of the evolutionary mechanisms which brought

them to their current state.

In this thesis I focus on one species of auk, the Crested Auklet. Crested Auklets are socially monogamous, ornamented, colonial seabirds that lay a clutch size of one and have semi-precocial chicks that are provisioned by both parents at the crevice nest site (Jones 1993b; Gaston and Jones 1998). This species represents one component of a remarkable adaptive radiation of five small planktivorous auklets (including Whiskered [*A. pygmaea*], Least [*A. pusilla*], Parakeet [*Cyclorrhynchus psittacula*] and Cassin's [*Ptychoramphus aleuticus*] auklets) endemic to the North Pacific Ocean and Bering and Okhotsk Seas. Very little is known about Crested Auklets outside of the breeding season and much of what is known of their breeding season activities comes from St. Lawrence Island in the northern Bering Sea.

Seabirds are long-lived and can have large inter-year variation in chick quality, chick prey types and reproductive success, therefore it is important to obtain basic baseline data which shows the extent of inter-year variability, ideally from different breeding sites of the species' range. In the first paper I present and discuss three years (1996 to 1998) of Crested Auklet chick growth data from two different colonies in the Aleutian Island chain (Buldir, 52° 21'N, 175° 56'E and Kasatochi, 52°11'N, 175°30'W islands) and nine-years of productivity and breeding chronology data from Buldir. This paper is the first to offer inter-island and inter-colony comparisons of breeding parameters of Crested Auklets from the Aleutian Islands which comprise a substantial portion of this species' range.

Once baseline data are collected we can begin further detailed investigations into the mechanisms of how a species reproduces, how they rear their young and what criteria they use in mate choice. For example, an understanding of the relationship between provisioning rates and how they or if they relate to chick fledging age (i.e. length of stay at the nest site) could lead to considerable insight to understanding the differences among the auk species in their reproductive strategies. In my second paper I investigate the roles of male and female Crested Auklets in parental care during the chick rearing period. This species is unusual among auks for the noticeable sexual dimorphism in bill shape and size: males have a longer culmen, a larger bill depth than females and a hook at the end of their bill (Jones 1993a; Gaston and Jones 1998 [illustration]). I examined prey selection by males and females for chick provisioning and examined the specific roles they have during chick rearing to help elucidate whether these bill shape differences evolved from male intra-sexual selection (Jones and Hunter 1999) or from ecological niche divergence (Shine 1989).

Clutton-Brock and Godfray (1993) defined parental care as any behaviour which is likely to increase the fitness of a parent's offspring. The level of parental care provided by an individual is likely to be influenced by many different factors including confidence of paternity, inter-sexual differences in size or aggressiveness that affect their performance in the role of guarding offspring (e.g. Burger 1981), ecological constraints, such as food availability (e.g. Uttley 1992) and mate attractiveness ("differential allocation hypothesis": Burley 1986, 1988; deLope and Møller 1993).

According to the differential allocation hypothesis, an individual invests more in parental care than their attractive partner to maintain the pair bond. Trivers (1972) and Williams (1966) both developed models that examined the relationship between sexual selection and parental investment and predicted that in species where males and females have similar investment in offspring, both sexes should also be equally discriminating about their prospective mate. Quantification of parental effort may provide a relative measure of the opportunity for sexual selection to operate with each sex for a given species (Trivers 1972).

In my third paper I investigate the relationships between parental effort, mate retention and ornamentation. Research by Burley (1986, 1988) and de Lope and Møller (1993) has indicated that some ornamented, socially monogamous bird species adjust the level of parental care according to their mate's attractiveness. Here, I present the first data that investigates the differential allocation hypothesis (Burley 1986) for naturally occurring ornament variation in the Crested Auklet. Years of seabird research have demonstrated that pair breeding success often has a direct influence on mate choice and mate retention (reviews by Rowley 1983 and Choudhury 1995) and I examine what the benefits are for mate retention in Crested Auklets and whether mate retention is related to degree of ornamentation.

BREEDING BIOLOGY OF CRESTED AUKLETS AT BULDIR AND KASATOCHI ISLANDS, ALASKA

ABSTRACT

I quantified breeding parameters of the Crested Auklet (*Aethia cristatella*), at Buldir and Kasatochi islands in the Aleutian Islands, Alaska from 1996 to 1998. Crested Auklets incubated their eggs for about 36 days and their chicks weighed about 36 g within the first three days of hatching (14% of adult mass, Buldir n = 92). Growth rates averaged 9.98 g/day during the linear phase (Buldir n = 98; Kasatochi n = 24) and chicks fledged at an average mass of 247 g (95% of adult mass, Buldir n = 96) and a wing length of 124 mm (88% of adult wing length, Buldir n = 70) at 34.5 days after hatching. On Buldir, I found significant inter-year differences in hatch and fledge dates, linear growth of wing and maximum mass. On Kasatochi, I found inter-year differences of linear growth of mass. Productivity (the product of hatching success and fledging success) averaged over 65% for three years (1996 to 1998) at Buldir and Kasatochi. Inter-colony comparisons of productivity parameters revealed differences in hatch date, fledge date, age of chicks at fledging and both hatching and fledging success. At Buldir I observed no negative effect of various levels of investigator disturbance on hatching and fledging success or on other breeding parameters. I found no negative relationships between hatch date and fledging age, hatch date and fledging mass or fledging mass and fledging age, contrary to the predictions of Ydenberg's model of intra-specific variation in timing of fledging of alcid chicks. Crested Auklet chicks, like those of other diurnally active auklet species, grow relatively fast and depart at a younger age compared to the chicks of two auklet species that attend their

colonies only at night.

INTRODUCTION

Crested Auklets (*Aethia cristatella*) are colonial seabirds that lay a clutch size of one and have semi-precocial chicks that are provisioned by both parents at the crevice nest site (Jones 1993b, Gaston and Jones 1998). This species represents one component of a remarkable adaptive radiation of five small planktivorous auklets (including Whiskered [*A. pygmaea*], Least [*A. pusilla*], Parakeet [*Cyclorrhynchus psittacula*] and Cassin's [*Ptychoramphus aleuticus*] auklets) endemic to the North Pacific Ocean and Bering and Okhotsk Seas. These auklets range in mean body mass from the Least Auklet at 85 g to the Parakeet Auklet at 289 g. Adult and chick diets and chick development patterns (Gaston 1985, Gaston and Jones 1998) also vary among species. The biology of nocturnal Cassin's and diurnal Least Auklets has been relatively well-studied (summarized by Manuwal and Thoresen 1993 and Jones 1993c), whereas Parakeet and Crested Auklets are less well known (Bédard 1969a; Hipfner and Byrd 1993; summary in Jones 1993b) and the nocturnal Whiskered Auklet is the least well known (Byrd and Williams 1994). Detailed knowledge of the biology of all auklet species is required for an understanding of their life-history variation, adaptive radiation and ecological relationships.

Alcids show considerable inter- and intra-specific variability in the age and mass of their chicks at the time of departure from their nest sites at the colony for the sea. For

example, the tiny precocial chicks of Ancient Murrelets' (*Synthliboramphus antiquus*) depart two days after hatching, whereas the semiprecocial chicks of Rhinoceros Auklets (*Cerorhinca monocerata*) depart close to adult size at 38 to 58 days old (Gaston 1985, Gaston and Jones 1998). Ydenberg (1989) and Ydenberg et al. (1995) provided the first comprehensive model that explained Alcid life history variation and intra-specific variability and offered testable predictions. Two main assumptions of the model were that juvenile mortality is lower at the nest while growth is higher at sea. Here, I test two of the model's predictions about intra-specific variation in life-history traits using data from Crested Auklets: 1) fast growing chicks depart the nest younger and heavier (i.e. a negative relationship between fledging age and fledging mass), and 2) late-hatching chicks depart younger and lighter. Although some data from Cassin's and Rhinoceros Auklets were consistent with these predictions (Harfenist 1995, Harfenist and Ydenberg 1996, Morbey and Ydenberg 1997), further testing of the model is needed (Gaston and Jones 1998, Hipfner and Gaston 1999). Crested Auklet chicks are semi-precocial, depart close to adult size, fit all of the assumptions of the model (Ydenberg et al. 1995) and thus provide an opportunity to examine the model's predictions for the first time within the genus *Aethia*.

Much of the information on Crested Auklet breeding parameters comes from northern colonies on St. Lawrence Island (Bédard 1969a, Piatt et al. 1990) where the birds nest later than their Aleutian counterparts in the presence of mammalian predators. The Aleutian Islands comprise a substantial portion of the Crested Auklet's breeding range.

Nevertheless, Knudtson and Byrd's (1982) and Hipfner and Byrd's (1993) work on laying and hatching dates, productivity and crevice attributes of Crested Auklets provide the only published data from the Aleutians, which lacks mammalian predators. Here, I present the first comparisons across years and colonies of chick growth, productivity and breeding chronology in Crested Auklets, including nine years of data from a single colony in the Aleutians.

Breeding biology characteristics such as chick growth and productivity are crucial parameters for any species, but are particularly important for species influenced by complex ecological changes resulting from management of other species in their community. In the Bering Sea, intense commercial fishing for walleye pollock (*Theragra chlacogramma*), Pacific cod (*Gadus macrocephalus*) and Salmon (*Onchorhynchus* spp.), directly alter the community's trophic relationships and may indirectly affect seabird populations (e.g. Springer et al. 1987, Springer 1991). Auklets are important predators of zooplankton in the marine food web, and a more complete understanding of the range of variation that exists in their breeding parameters and how these parameters may be affected by changes in their ecosystem will be helpful in evaluating impacts of perturbations like commercial fisheries.

The objectives of my study were to (1) quantify chick growth and present inter-colony and inter-year comparisons for three study years (1996 to 1998); (2) examine nine years of variation in reproductive performance and breeding chronology from one colony in the western Aleutians (1990 to 1998) and make inter-year and inter-colony

comparisons with another site located in the central Aleutians (1996 to 1998); (3) evaluate the affects of investigator disturbance on breeding success and (4) test two key predictions of Ydenberg's (1989) model to explain timing of chick departure for a semi-precocial species of auklet.

STUDY AREA AND METHODS

I studied auklets on Buldir (52° 21'N, 175° 56'E) and Kasatochi (52°11'N, 175°30'W) islands in the Aleutians chain of Alaska (Fig. 2.1). Buldir, located in the western part of the island chain, contains one of the largest and most diverse seabird concentrations in the Aleutians (Sowls et al. 1978, Byrd and Day 1986). My study area on Buldir was located at "Main Talus", a 4.3 ha colony with approximately 250,000 Crested and Least Auklets (2:1 Crested to Least, Knudtson and Byrd 1982, Byrd et al. 1983). Kasatochi is located in the central Aleutians about 480 km east of Buldir. The study area there was in a auklet colony on a northeast-facing talus slope with a minimum of 35,000 Least and Crested Auklets (2:1, Least to Crested; Scharf et al. 1996).

Chick growth, productivity and breeding chronology were recorded on both islands while investigator disturbance was evaluated on Buldir only. I selected crevices which were configured so that parents or chicks in nest sites could not easily hide from view. Because my samples of crevices were taken from large areas and were of different crevice types (except for very deep crevices) I believe the crevices

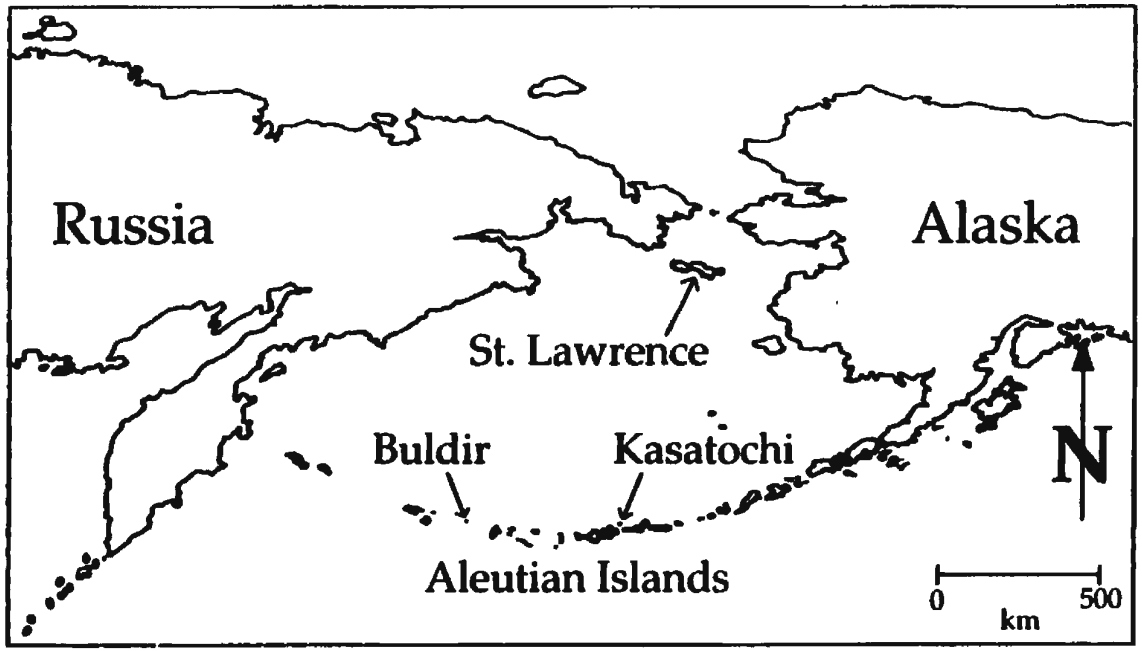

Figure 2.1. Map that includes both of my two study sites in the Aleutians and St. Lawrence Island.

monitored were representative of the entire colonies at Buldir and Kasatochi. For all crevices, chicks were considered fledged if they were 26 days or older upon disappearance (i.e. the crevice failed if chick < 26 days) because they were fully feathered by this age.

Incubation and Chick Growth

In 1997 (n = 8) and 1998 (n = 26) I followed pairs from laying until hatching to determine incubation duration on Buldir. I selected previously used crevices that were unoccupied in mid-May and checked them daily until an incubating bird was present. To minimize disturbance early in incubation, I checked occupied crevices weekly for the first 29 days. After 29 days, I checked crevices daily to obtain the exact date of hatching. During 1997 and 1998 I also measured egg size (eggs measured by Fiona M. Hunter and Ian L. Jones). I removed and measured egg length and width using a calipers, from incubating birds (using auklet crevices other than the ones used for the rest of the study), then returned the eggs to their crevices. I also opportunistically measured eggs that were abandoned or found on the talus.

From 1996 to 1998, I studied chick growth on Buldir and Kasatochi Islands. Because I had larger sample sizes and wanted more precise data from Buldir, my method varied slightly between the two colonies. To determine the date of hatching on Buldir, nests were checked once a week until mid-June (again to minimize disturbance early in the incubation period), then every two days until hatching. Chick age was estimated to within one day based on appearance (Jones 1993b). Chicks

were then measured every three days until they departed from their crevice; in most cases fledging dates were known to nearest day. On Kasatochi, date of hatching was determined by checking nests at four-day intervals prior to hatching and estimated chick age to within two days. I measured chicks only during the linear growth period on Kasatochi; therefore chicks were handled every four days (from ages 6 to 24 days) and fledging dates were estimated to within two to four days. I measured chick mass to the nearest 1 g, flattened wing (Buldir) and wing chord (Kasatochi) to the nearest 1 mm and tarsus length to the nearest 0.1 mm.

I used regression residuals from mass versus age and wing versus age to estimate the linear portion of the growth curve from composite data. I assumed linear growth when the residuals were randomly distributed around zero. The slopes of simple linear models for mass and wing from each chick provided comparative statistics. The sample units were individual chicks with at least three measurements collected during the linear growth period. I used $P < 0.05$ as a threshold for concluding statistical significance.

To compare the growth data with those studies of Crested Auklets on St. Lawrence Island (Sealy 1968, Piatt et al. 1990) I fitted individual growth data from Buldir (1996 and 1997) to a logistic model (Ricklefs 1967). The model's products (asymptotic weight [a] and k) were used to calculate the instantaneous growth rate at the point of inflection (Ka/4, Hussell 1972), which is considered to be the maximum growth rate (Hussell 1972, Sealy 1973a, Gaston 1985, Piatt et al. 1990).

Adult Mass

To quantify variation in adult mass within and between breeding seasons and islands and to compare adult mass with the chick mass at fledging, I caught birds at a single study plot centrally located on Main Talus, Buldir Island, and at a similar plot on Kasatochi Island. I determined the sex of these birds using bill shape (Jones 1993a) and weighed them to the nearest g with a spring scale. On both islands adult measurements were taken between May and August from 1996 to 1998.

Productivity and Breeding Chronology

Crested Auklet crevices were checked approximately every seven days throughout each breeding season between 1990 and 1996 (1996 at Kasatochi). In 1997, I began to check crevices every four days between the onset and termination of hatching and fledging periods to obtain more precise estimates of the timing of these events. To minimize bias due to nest failure early in the breeding season (i.e. an overestimation of hatching success), only crevices found prior to June 15 were used to estimate productivity. I used the mid-point between visits to estimate the dates of hatching and fledging dates and the even-numbered Julian date when an even number of days occurred between visits.

Effects of Investigator Disturbance

I evaluated the disturbance caused by my monitoring activities by comparing success of nests visited at different frequencies during the incubation and chick growth periods. In 1996, I visually checked crevices during incubation (1) once a week (low

disturbance), (2) every two days (medium disturbance) or (3) twice a day, (high disturbance). During 1997 and 1998 I had two levels of disturbance during the incubation period (1) every four to seven days checks (low disturbance) and (2) every two days (medium disturbance). During the chick-rearing periods of all years, I evaluated three levels of disturbance (1) crevices that we visually checked approximately every four to seven days (low disturbance), (2) crevices in which we captured a chick every three days (medium disturbance) and (3) crevices in which chicks were captured every three days and in which I captured at least one adult once within six days after hatching. To assess the effects of handling chicks in 1997 and 1998 I compared mass, wing and tarsus measurements of chicks handled regularly throughout the rearing period with chicks that I visually checked every three days, but captured and measured only once between ages 28 to 30 (i.e. control chicks).

RESULTS

Incubation and Chick Growth

In 1997, the duration of incubation averaged 35.9 $\pm$ 4.8 days (n = 8, range 29 to 44 days) and in 1998, 36.3 $\pm$ 1.7 days (n = 26, range 31 to 38) and did not differ significantly between years (P = 0.7). Egg size differed significantly between years; 1998 birds had larger eggs (t = -2.2, df = 70, P = 0.03; length x width, $\bar{x}_{1997}$ = 36.6 $\pm$ 2.8, n = 41; $\bar{x}_{1998}$ = 38.0 $\pm$ 2.6, n = 31).

On average, Buldir Crested Auklet chicks weighed about 36 g within three days of

hatching (13.7% of adult mass) and gained mass at approximately 10 g/day during the linear phase of growth (Table 2.1). They remained in their crevice for about 35 days (range 26 to 41 days) and fledged with wing lengths of 124 mm (88% of adult wing length, Fig. 2.2) and at a mass of 247 g (94% of adult mass, Tables 2.1 and 2.2, Figs. 2.3 and 2.4). Chick mass declined prior to fledging by 5% in 1996, 3% in 1997 and 12% in 1998.

At Buldir, I found no significant differences among years for hatch mass ($P = 0.06$), linear growth rate of mass ($P = 0.8$), fledge mass ($P = 0.9$) and fledge age ($P = 0.2$). There was a significant difference in hatch date ($F = 81.6$, df = 2 and 126 $P < 0.0001$; Fisher's PSLD, 1996 vs 1997, $P = 0.006$; 1996 vs 1998, $P < 0.0001$; 1997 vs 1998, $P < 0.0001$; Table 2.1), fledge date ($F = 41.5$, df = 2 and 102, $P < 0.0001$; *post hoc* tests 1996 vs 1997, $P = 0.02$; 1996 vs 1998, $P < 0.0001$; 1997 vs 1998, $P < 0.0001$; Table 2.1) and maximum mass ($F = 6.8$, df = 2 and 95, $P = 0.002$; *post hoc* tests 1996 vs 1997, $P = 0.3$; 1996 vs 1998, $P = 0.02$; 1997 vs 1998, $P = 0.0005$) between years. I found no significant relationships in any study year between hatch dates and the following: fledging mass, fledging age, fledging wing and linear growth rate for mass (Table 2.3). When linear growth was held constant in 1997 and 1998, I found that fast growing chicks fledged at a heavier mass, but not at an earlier age (i.e. a positive relationship between linear growth and fledging mass existed, but none between hatch date and fledging mass, or fledging age; Table 2.3). I also found a significant negative relationship (1997: $r^2 = 0.32$, $P = 0.02$, $n = 17$; 1998: $r^2 = 0.43$, P

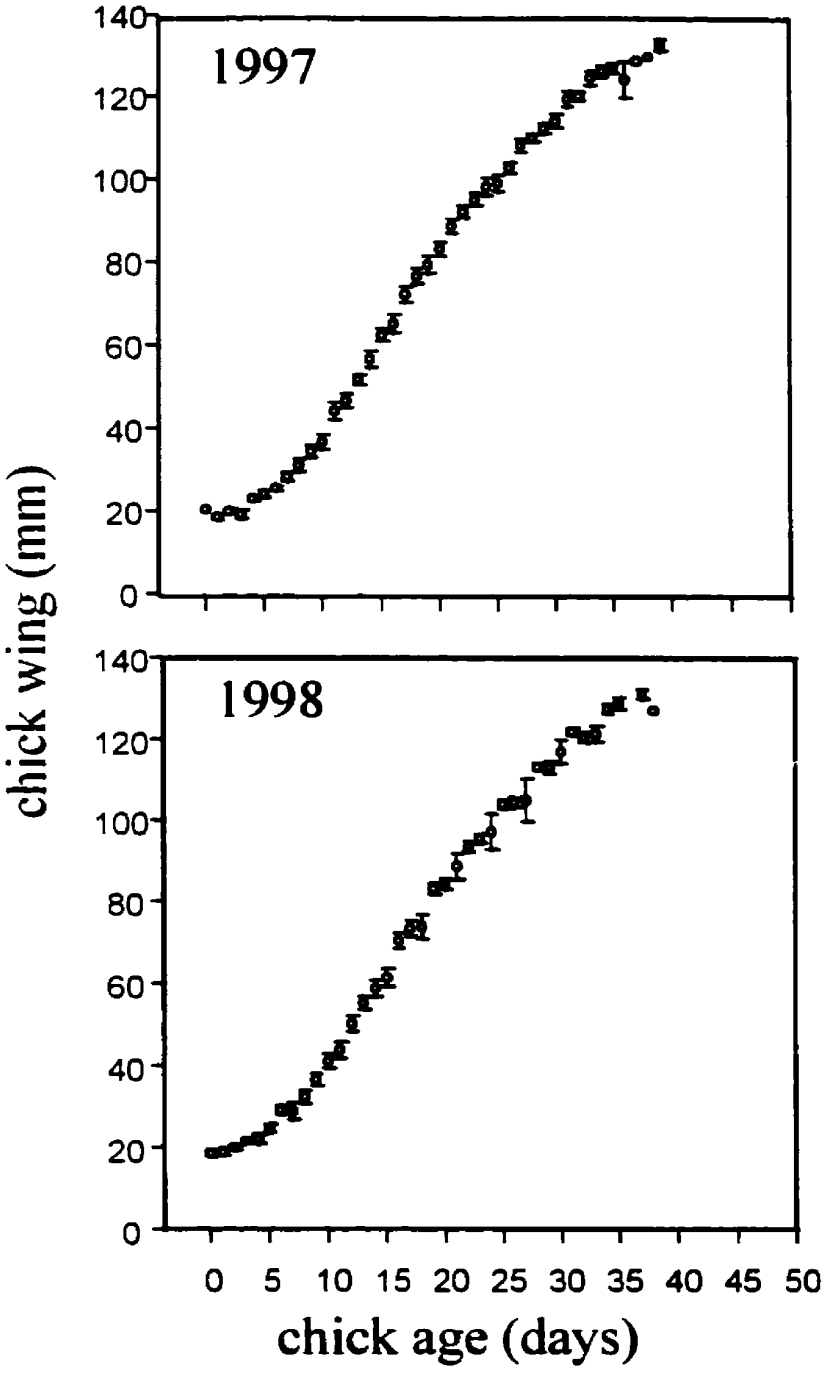

Figure 2.3. Mean (± SE) wing of Crested Auklet chicks over days for1997 to 1998, Buldir Island, Alaska.

Table 2.1. Summary of Buldir chick growth 1996 to 1998

	Hatch Date	Hatch Mass (g)	Hatch Wing (mm)	Slope Mass (g/day)	Slope Wing (mm /day)	Max Mass (g)	Age Max Mass (days)	Fledge Age (days)	Fledge Date	Fledge Mass (g)	Fledge Wing (mm)
1996											
mean	26 Jun	37.72	----	9 8	----	261 0	29.3	33.9	1 Aug	248.8	----
SD		10.95		1.45		36 6	3.3	3.74		31.33	
range		22-60		7 5-12.3		199-329	25-35	27-40		173-298	
N	45	29		27		30	30	30	30	26	
1997											
mean	24 Jun	33 13	19 6	10.1	4.5	252 0	30.1	35.3	30 Jul	245 8	123.4
SD		7.9	1.9	1 7	0 36	32.2	3.6	3.2		27	8 3
range		20-51	15-23	7 4-13.7	3 7-5 1	195-298	20-35	26-41	37	195-298	102-135
N	46	29	27	33	35	32	32	37		37	37
1998											
mean	7 Jul	38.3	19.7	10.0	4.2	278.1	28	34.3	10	247.4	125.3
SD		8.5	1.7	1 5	0.26	25.2	3.2	2.7	Aug	29 8	5 5
range		23-60	15-23	6.0-12.6	3.5-4.6	4.2	21-35	27-39		201-312	111-133
N	38	34	34	38	38	36	36	38	38	33	33

Table 2.2 Buldir Crested Auklet chick growth data fit to a logistic model and a comparison to St. Lawrence Island chicks.

Parameters	Asymptote a (g)	Adult Mass[a] *M* (g)	Fledge Age (days)	Fledging Mass *FM* (g)	*FM* / M (%)	K[b]	Ka[c] (g/day)	Author
Mean	254.4	286	34	228	80	0.197	12.5	Sealy 1968,1973
Mean	269	260-283	-----	-----	---	---	12.8	Piatt et al. 1990
Mean	---	267.1	---	---	---	---	11.1	Searing 1977
Mean	260.8	262.0	34	248.8	93	0.18	12.0	This study,
(S.D.)	(35.9)		(3.74)	(31.3)		(0.03)		1996
N	20	174	30	26	na	20	na	
Mean	258.5	262.0	35	245.8	94	0.17	11.1	This Study
(S.D.)	(34.1)		(3.2)	(27.0)		(0.04)		1997
N	35	174		37	na	35	na	

[a]Mass from incubating adults (see Fig. 2).
Mean Instantaneous growth rate calculated from individual chicks fit to the model.
[c]Maximum instantaneous growth (Hussel 1972, Sealy 1973a).

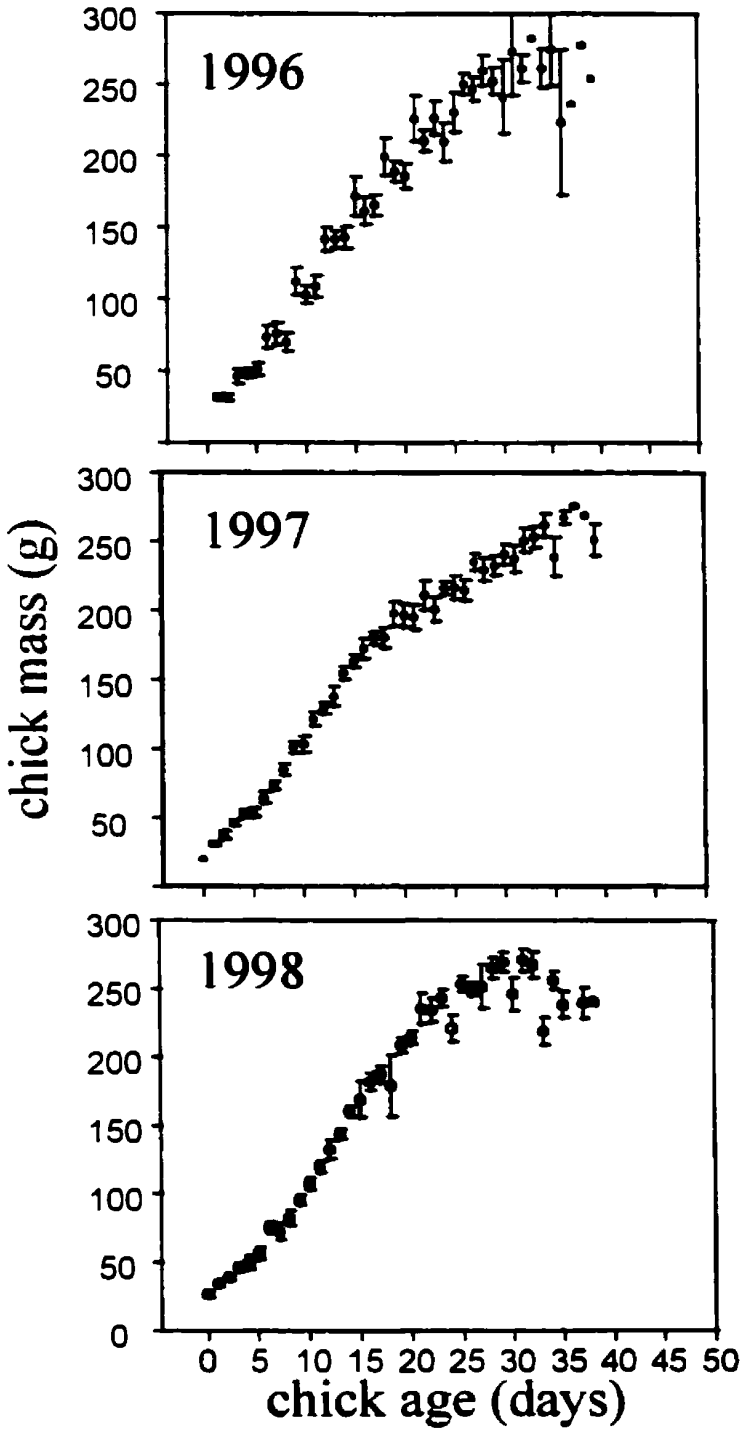

Figure 2.3. Mean (± SE) mass of Crested Auklet chicks over days for1996 to1998, Buldir Island, Alaska.

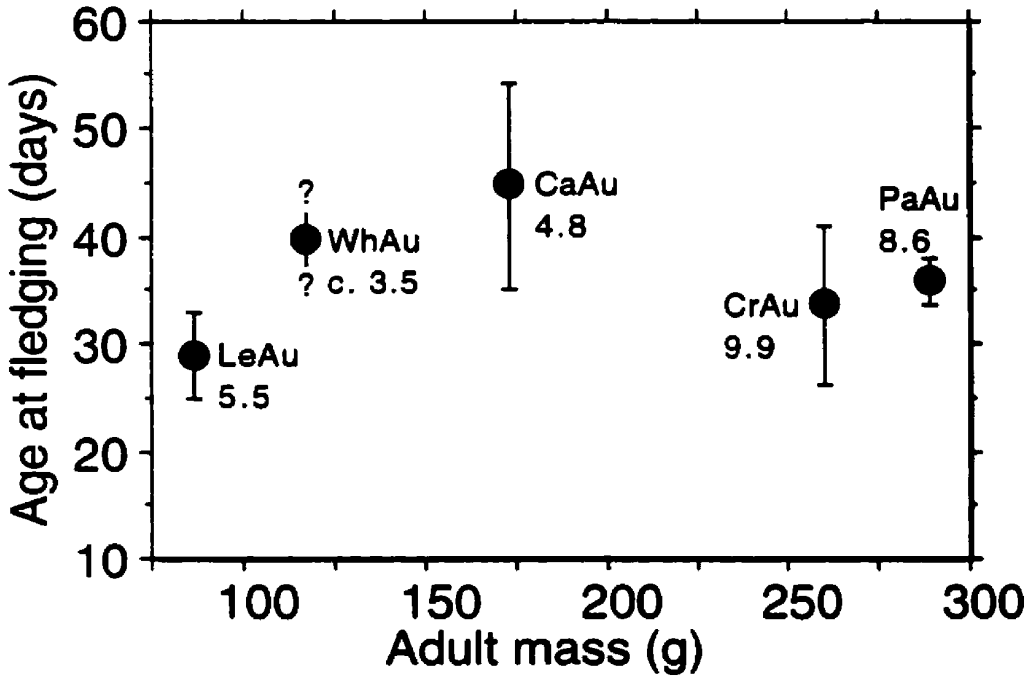

Figure 2.4. The relationship between adult mass, fledging age (bars indicate range of values recorded in published studies) and maximum growth rate (g/day) of chicks for the auklets Aethiiini (for reference see Gaston and Jones 1998)

Table 2.3. Results of the intraspecific predictions tested from Ydenberg's model.

		Hatch date			Hatch date, Linear growth of mass			Linear growth of mass		
Dependent variable	year	*n*	P	r^2	*n*	P	r^2	*n*	P	r^2
Fledging mass	1996	25	0.8	0.003	25	0.8, 0.3	0.05	23	0.3	0.04
	1997	35	0.2	0.04	35	0.5;0.02*	0.14	35	0.01*	0.18
	1998	32	0.3	0.03	32	0.5,0.02*	0.19	32	0.01*	0.18
Fledging age	1996	25	0.8	0.01	25	0.6; 0.4	0.04	26	0.4	0.03
	1997	35	0.9	0.001	35	0.9; 0.7	0.01	35	0.6	0.01
	1998	37	0.1	0.06	37	0.1; 0.5	0.07	32	0.6	0.006
Fledging wing	1996	---	---	---	---	---	---	---	---	---
	1997	35	0.4	0.02	35	0.3, 0.5	0.04	35	0.6	0.01
	1998	32	0.3	0.03	32	0.4, 0.4	0.06	32	0.3	0.03
Linear growth of mass	1996	24	0.7	0.01	---	---	---	---	---	---
	1997	32	0.1	0.09	---	---	---	---	---	---
	1998	32	0.5	0.01	---	---	---	---	---	---

= 0.002, n = 18) between wing length and age of fledging (i.e. day 25 which is one day before the first fledging age; see Hipfner and Gaston 1999). However, no significant relationship was found between mass and age of fledging (age 25 only) in any study year (1996: P = 0.6; 1997: P = 0.1; 1998: P = 0.2).

On average, Crested Auklets chicks at Kasatochi Island gained mass at approximately 10 g day during the linear growth phase and remained in their crevice for 34 days (range 26 to 40; Table 2.4). On Kasatochi, a significant effect of years was found for the linear growth of mass (F = 4.06, df = 2 and 21, P = 0.03; Fisher PLSD, 1996 vs 1997, P = 0.2; 1996 vs 1998, P = 0.2; 1997 vs 1998, P = 0.01) and for linear growth of wing (F = 4.5, df = 2 and 21, P = 0.02; Fisher PLSD, 1996 vs 1997, P = 0.04; 1996 vs 1998, P = 0.5; 1997 vs 1998, P = 0.01), but not for fledge date (P = 0.6) or for fledge age (P = 0.5).

Adult Mass

On average, male Crested Auklets ($\bar{x}$ = 267 ± 19 g, range 211 to 345, n = 353) were 14 g heavier than females ($\bar{x}$ = 253 ± 17 g, range 210 to 322, n = 352; t = 10.1, df = 1, P < 0.0001, Fig. 2.5). On Buldir, mass also varied significantly among years (1990 to 1997; F = 6.2, df = 6 and 565, P < 0.0001), being highest in 1997 and 1993, which corresponded with two years of high breeding productivity (Table 2.5). I examined inter-island and inter-year differences for adult mass from 1996 to 1998 and found that island and year were significant as main effects and in interactions (two-way ANOVA, island, F = 5.3, df = 1 and 648, P = 0.02; year, F = 5.0, df = 2 and 648, P

Table 2.4. Summary of Kasatochi Crested Auklet chick growth 1996 to 1998.

	Hatch Date	Slope Mass (g/day)	Slope Wing (mm/day)	Fledge Age (days)	Fledge Date
1996					
mean	30 Jun	10.2	3.7	33.8	2 Aug
SD		2.6	0.32	3.4	
range		7.7-12.7	3.2-3.9	26-40	
N	7	7	7	6	6
1997					
mean	2 Jul	8.54	3.17	35.6	6 Aug
SD		2.6	0.6	5.7	
range		4.0-11.7	1.9-3.9	27-36	
N	10	10	10	8	8
1998					
mean	3 Jul	11.7	3.8	33.4	6 Aug
SD		1.8	0.25	2.7	
range		9.3-15.3	3.6-4.1	28-36	
N	9	7	7	7	7

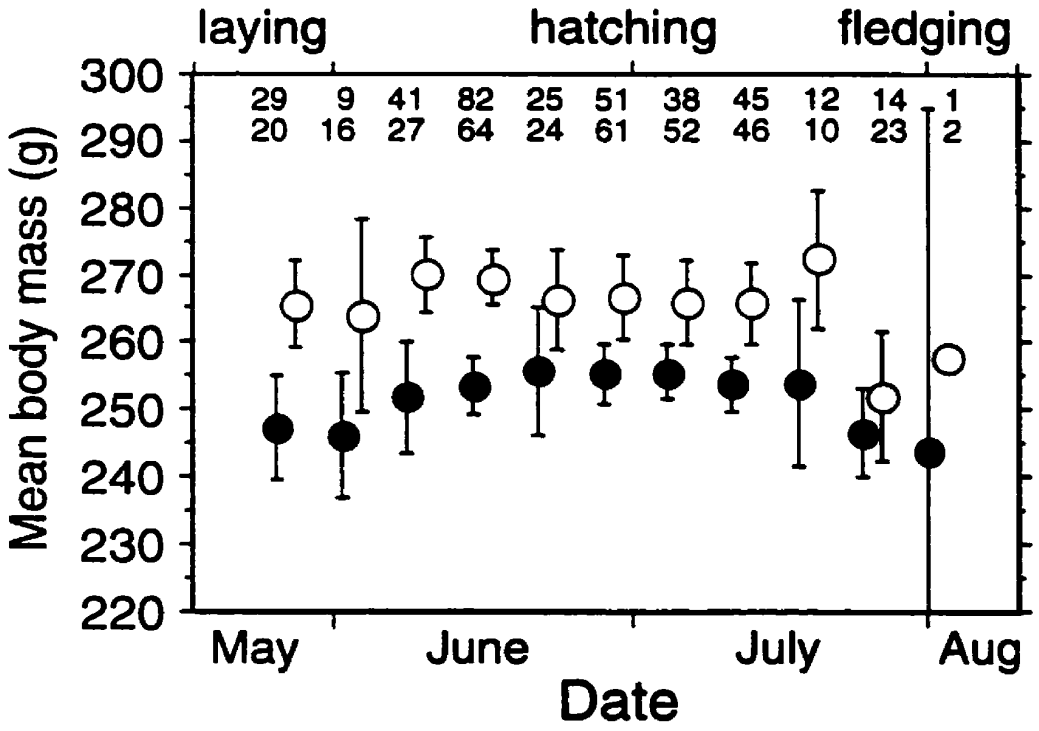

Figure 2.5. Variation in mass of male (open circle) and female (closed circle) adult Crested Auklets at Buldir and Kasatochi Islands, Alaska (means ± 95% confidence limits, sample sizes indicated for each week).

Table 2.5. Reproductive performance and variation of adult mass of Crested Auklets at Buldir Island, Alaska.

Parameter[a]	1990	1991	1992	1993	1994	1995	1996	1997	1998
No. eggs found (A)	67	74	79	49	67	66	66	82	70
No. of eggs hatched (B)	49	56	70	44	59	59	57	77	62
Median hatch date	21 Jun	30 Jun	27Jun	24 Jun	25 Jun	26 Jun	29 Jun	25 Jun	7 Jul
(range)	21 Jun - 19 Jul	21 Jun- 12 Jul	12 Jun - 7 Jul	16 Jun - 15 Jul	14 Jun - 15 Jul	21 Jun - 21 Jul	16 Jun - 12 Jul	15 Jun 15 Jul	20 Jun - 21 Jul
No. chicks lost to:									
disappearance	13	12	12	6	9	7	9	14	9
death	3	1	1	0	4	1	8	1	0
Median fledge date	29 Jul	1 Aug	26 Jul	27 Jul	28 Jul	30 Jul	3 Aug	29 Jul	11 Aug
(range)	19 Jul >1 Aug	25 Jul -8 Aug	13 Jul - >10 Aug	23 Jul - >31 Jul	15 Jul - 14 Aug	26 Jul - 16 Aug	20 Jul - 14 Aug	16 Jul- 8 Aug	27 Jul - 19 Aug
No. chicks fledged (C)	33	43	57	38	46	51	40	62	53
Hatching success (B/A)[b]	0.72	0.76	0.87	0.9	0.88	0.89	0.86	0.94	0.89
Fledging success (C/B)[c]	0.69	0.77	0.81	0.86	0.78	0.86	0.70	0.81	0.85
Productivity (hs x fs)	0.49	0.59	0.70	0.78	0.69	0.77	0.60	0.76	0.76
Adult Mass									
mean male	260.8	259.4	266.6	273.5	264.8	268.2	267.1	267.6	271.2
SD	23.0	16.5	16.4	18.0	19.9	21.3	18.1	19.7	19.3
n	17	16	58	48	41	44	49	63	113
mean female	252.1	252.4	246.9	260.5	258.4	250.9	253.2	253.5	252.5
SD	20.6	22.7	15.8	13.6	11.5	18.1	14.4	19.7	20.9
n	30	14	42	38	5	55	62	42	169

= 0.007; island*year, F = 7.9, df = 2 and 648, P = 0.0004; Fisher PLSD, island, P = 0.06. Buldir: $\bar{x}_{1996}$ = 259 ± 17, $\bar{x}_{1997}$ = 261 ± 20, $\bar{x}_{1998}$ = 260 ± 21; Kasatochi: $\bar{x}_{1996}$ = 265 ± 16, $\bar{x}_{1997}$ = 251 ± 17, $\bar{x}_{1998}$ = 251 ± 16)

Productivity and Breeding Chronology

Over a nine-year period at Buldir, Crested Auklet productivity, averaged 86% for hatching success, 79% for fledging success and 68% for productivity (Table 2.5). I examined fledging success for each island for the three study years and found that hatching and fledging success for both islands did not significantly differ among years (P > 0.05; Table 2.5). For the three study years on Kasatochi (1996 to 1998), Crested Auklets averaged 86% hatching success, 76% fledging success and 65% for productivity (Table 2.6).

The annual breeding chronology for Crested Auklets on Buldir varied during the nine years I monitored the colony (Table 2.5).The median hatching date was 26 June, but hatching dates varied by 16 days among years; typically the first eggs hatched in mid-June, the last eggs hatched in mid-July. Median fledging dates differed as much as 15 days between breeding seasons, but generally the first chicks fledged about 20 July, the last chicks fledged around 13 August. On average, the auklets on Kasatochi appeared to be on a slightly later schedule than Buldir (Table 2.6). The first chicks hatched on 26 June, the last chicks on 17 July and the median hatch date was 1 July. The first chicks fledged on 22 July, the last ones by > 16 August and the median fledging date was 5 August.

Table. 2.6. Reproductive performance and variation of adult mass of Crested Auklets for Kasatochi Island, Alaska.

Parameter	1996	1997	1998
No. eggs found (A)	43	76	104
No. of eggs hatched (B)	37	64	91
Median hatch date	Jun 30	Jul 1	Jul 3
range	Jun 26-Jul 17	Jun 27-Jul 14	Jun 29-Jul 15
No. chicks lost to:			
disappearance	2	13	14
death	3	9	8
Median fledge date	Jul 31	Aug 8	Aug 8
range	Jul 22-Aug 8	Jul 27-Aug 12	Jul 31->Aug 16
No. chicks fledged (C)	32	42	69
Hatching success (B/A)[a]	0.86	0.84	0.88
Fledging success (C/B)[b]	0.86	0.66	0.76
Productivity (hs x fs)	0.74	0.55	0.67
Adult mass			
mean male	269.1	256.2	258.4
SD	17.6	18.6	12.8
n	29	19	27
mean female	261.7	248.8	247.4
SD	19.5	15.1	16.2
n	30	31	14

Inter-island Comparisons of Breeding Chronology and Productivity

In comparing reproductive variables for six colony-year combinations, (Buldir and Kasatochi in 1996, 1997 and 1998) I found significant interactions for: hatching date (F = 13.5, df = 2 and 376, $P < 0.0001$; Tables 2.5 and 2.6), fledging age (F = 21.7, df = 2 and 287, $P < 0.0001$; 1996: $\bar{x}_{Buldir}$ = 35.2 days, $\bar{x}_{Kasatochi}$ = 31.7 days; 1997: $\bar{x}_{Buldir}$ = 32.6 days, $\bar{x}_{Kasatochi}$ = 34.0 days; 1998: $\bar{x}_{Buldir}$ = 34.2 days, $\bar{x}_{Kasatochi}$ = 32.7 days) and fledging date (F = 42.7, df = 2 and 287, P < 0.0001; Tables 2.5 and 2.6). Hatching and fledging success were significantly different between islands for 1997 (hatching: X^2 = 3.86, P = 0.05; fledging: X^2 = 4.0, P = 0.05), but not for 1996 or 1998 (1996: hatching success, X^2 = 0.02, P = 0.9; fledging success, X^2 = 3.3, P = 0.06; 1998: hatching success, X^2 = 0.05, P = 0.8; fledging success, X^2 = 2.1, P = 0.1; Tables 2.5 and 2.6).

Effects of Investigator Disturbance

Crested Auklets tolerated large amounts of disturbance during the incubation period: hatching success did not differ significantly (P = 0.2) with low (86% hatching success, n = 66, Table 2.5), medium (91%, n = 40) or high levels of disturbance for 1996 (100%, n = 20) or for low or medium levels of disturbance in 1997 (low, 94%, n = 82; medium, 89%, n = 54) or 1998 (low, 89%, n = 70; medium, 97%, n = 85). Crevices where I either captured an adult and/or handled a chick regularly did not experience lower fledging success in 1996 (low = 70.1%, n = 57; medium = 57%, n = 14; high = 73%, n = 26; P = 0.6) or 1998 (low = 86%, n = 62; medium = 50%, n = 6; high =

88%, n = 40; P = 0.06). In contrast, I did find differences in 1997 among the different levels of disturbance; crevices with a high level of disturbance achieved a higher fledging success (X^2 = 7.4, P = 0.03, low = 81%, n = 77; medium = 56%, n = 9; high = 92%, n = 39).

Crested Auklet chicks that were handled regularly were the same size between days 28 to 30 as chicks only handled once. Chicks only handled once (1997 and 1998 combined, control chicks, n = 29, measured between days 28 to 30) were similar in mass (P = 0.07; $\bar{x}_{control}$ = 263.3 g, $\bar{x}_{growth}$ = 250.4 g), wing (P = 0.4; $\bar{x}_{control}$ = 113.5 mm, $\bar{x}_{growth}$ = 112.3 mm), and tarsus (P = 0.7; $\bar{x}_{control}$ = 27.6 mm, $\bar{x}_{growth}$ = 27.7 mm) compared to chicks handled every three days (ages 28 to 30).

DISCUSSION

Incubation and Chick Growth

Similar to other studies (Sealy 1984, Piatt et al. 1990), I found that the duration of the incubation period to be highly variable, although mean duration on Buldir was comparable to that on St. Lawrence Island. I believe that the wide range in incubation periods was related to egg neglect, as Sealy (1984) reported for Crested and Least auklets and Ancient Murrelets and as Boersma (1982) for Procellariformes. Crested Auklet eggs can endure periods of cooling and still successfully hatch, I observed an egg (found unattended several times) hatch after 44 days. The ability of eggs to endure cooling periods is likely to be important for seabird species that forages far

from the colony on ephemeral patches of food. Egg neglect on the order of several hours or even days is not observed in passerine species in which prey is readily available on the territory and predation pressures are high (Drent 1975).

While Crested Auklet chicks on Buldir fledged at a similar age and grew at rates comparable to St. Lawrence Island chicks (Sealy 1968) fledging mass differed between the two sites (Sealy 1968, 1973a; Searing 1977). I would predict that fledglings on St. Lawrence would be heavier than fledglings on Buldir because adult mass, on average, was greater in the northern part of their range (Sealy 1968, Jones 1993b). However, St. Lawrence Island chicks weighed less at fledging (228 g) and lost more mass prior to fledging (11% mass decline) than chicks on Buldir (Sealy 1968, 1973a). The Ydenberg model (Ydenberg et al. 1995) for intra-specific variation predicts that in colonies with faster growth, nestlings will fledge heavier and younger; however Buldir chicks only fledged heavier, not at a younger age. There are three possible reasons for the observed differences in fledging mass between chicks from St. Lawrence Island and those from the Aleutians: (1) methods differed between the two studies (i.e. chicks that were handled every day fledged lighter than those handled less frequently), (2) environmental differences between the two areas resulted in the Aleutian chicks being fed more often or on higher quality food or (3) differences resulted from inter-year variation related to differences in prey availability.

Ydenberg's model (Ydenberg 1989, Ydenberg et al. 1995), concerning the transition from nest site to sea by alcid chicks, predicted three negative relationships: (1)

between hatch date and fledging mass, (2) between hatch date and fledging age and (3) between fledging age and chick growth. The model also predicted a positive relationship between observed fledging mass and chick growth. Studies on two semi-precocial species, Cassin's (Morbey and Ydenberg 1997) and Rhinoceros Auklets (Ydenberg et al. 1995, Harfenist 1995) supported the model's predictions. However, I found no significant negative relationships between these variables for Crested Auklets at Buldir Island in any of my study years. When linear growth of mass was controlled for, I only observed a positive relationship in 1997 and 1998 between linear growth and fledging mass which implied that faster growing chicks fledged heavier, but not earlier. The lack of seasonal decline in fledging mass at Buldir in 1996 and 1997 could have resulted from lack of strong seasonality in food abundance around this near-oceanic island. In 1998, I observed a stronger seasonal decline in fledging mass which corresponded with very late onset of breeding.

Hipfner and Gaston (1999) suggested that wing length is a better predictor of timing of chick departure than mass and predicted a negative relationship between wing length at minimum fledging age minus one day and fledging age. I observed this relationship for Crested Auklet chicks on Buldir. Crested Auklets had a higher survival rate if they were able to fly out to sea rather than walk, because fliers are more adept at both avoiding predators and at getting past the surf (G. Fraser personal observation; Jones 1993b). Therefore wing length might be more crucial than mass in determining the timing of Crested Auklet chick departure.

Among the five planktivorous auklet species (Crested, Least, Whiskered, Parakeet and Cassin's) that coexist in the Bering Sea and adjacent parts of the North Pacific, the major dichotomy in chick provisioning occurs between species with nocturnal versus diurnal colony attendance. The nocturnal colony attenders Cassin's and Whiskered auklets, which are constrained to feeding their chicks no more than once or twice per day during the hours of darkness, have relatively slow-growing chicks that fledge at 40 days or older, whereas the diurnal species (particularly Least Auklets) have relatively fast-growing chicks that fledge between 29 and 36 days after hatching. A nocturnal lifestyle for Cassin's and Whiskered auklets, while presumably reducing adult mortality from predation, prolongs the nestling period of their chicks (Sealy 1973). Diurnal activity at the colonies is the ancestral character state for planktivorous alcids (Gaston and Jones 1998). The evolution of nocturnal colony activity by these two species may have been favoured because it reduced competition for nest sites, permitted colonization of areas with large numbers of avian predators, and/or enhanced diurnal foraging opportunities.

Productivity and Breeding Chronology

Crested Auklet productivity and breeding chronology appeared to be somewhat flexible. Productivity on Buldir steadily increased for the first four years (1990 to 1993), then fluctuated in alternating years (1994 to 1998). A relationship between productivity and breeding chronology may exist: in two of three years, lower productivity corresponded with later hatching and fledging dates. Though there was

little difference in annual hatch dates, on Kasatochi, lower productivity coincided with a later fledging date. Knudtson and Byrd (1982) reported productivity from Main Talus on Buldir from 1976 as 51% (proportion of chicks fledged to number of eggs laid), which is 17% lower than average productivity during the 1990's. Lower productivity in 1976 also corresponded with a very late peak hatch date (July 8).

During my study, inter-colony and inter-year differences in productivity were dramatic. On Buldir, productivity increased by 27% between 1996 and 1997 while Kasatochi productivity dropped by 26%. The timing of breeding and the productivity of an auklet colony were almost certainly related to local prey availability and chick growth parameters from both islands rose and fell in tandem with the changes in productivity. It is also interesting to note that while Buldir experienced a very late breeding season in 1998, Kasatochi did not, which may be indicative of a local food availability phenomenon. Data on prey types, prior to and during chick rearing, between islands and years would allow me to further examine these relationships. Other factors that could influence timing and success of breeding are local weather conditions such as sea state, sea temperature, wind speed and rain fall during the winter and summer months.

Other Crested Auklet productivity data available for comparison are scarce. From St. Lawrence Island, Piatt et al. (1990) reported productivity for 1987 at 48% (proportion of chicks fledged to number of eggs laid). While this value fell within the observed range for Buldir (1990), it is 19% lower than Buldir productivity averaged

over the 1990s. One major difference between our two study sites and the colonies on St. Lawrence Island is a lack of mammalian predators. I would predict lower productivity values from those colonies that have mammalian predators present. Both Sealy (1968) and Piatt et al. (1990) documented vole (*Clethrionomys rutilus* and *Microtus oeconomus*) and arctic fox (*Alopex lagopus*) predation on chicks as important factors that depressed auklet productivity on the St. Lawrence Island colonies.

Effects of Investigator Disturbance

I found that investigator disturbance had little impact on hatching success (all years) and fledging success (two years). I did, however find marginal effects of disturbance in the fledging success in 1998 which may be related to the late breeding season. My findings were similar to that for Parakeet Auklets (Hipfner and Byrd 1993), but it differed from Piatt et al.'s (1990) at St. Lawrence where hatching and fledging success of Least Auklets decreased for their highly disturbed plots.Again, mammalian predation may explain the differences in our results; higher levels of disturbance to adults on St. Lawrence Island may have caused auklet chicks to be more vulnerable to mammalian predation.

Regular handling of chicks can often negatively influence chick growth and cause chicks to fledge prematurely (e.g. Harris and Wanless 1984, Lyngs 1994). However, I found no differences in tarsus length, wing length or mass between regularly handled chicks and chicks only measured once. This suggests that measuring chicks once

every three days is an appropriate protocol, though a longer interval between measurements during the linear growth phase would suffice (Harfenist 1995).

Conclusions

The paucity of data on Whiskered Auklet breeding biology presents the biggest gap of knowledge within the *Aethia* group; once that is bridged a more in-depth comparison of auklet life history strategies will be possible. Furthermore, an understanding of how productivity, breeding chronology and growth parameters correspond with inter-year variation in prey types, and ideally, how the availability of prey types changes throughout the seasons is essential for a comprehensive examination of auklet ecology, including how large changes in their marine ecosystem may influence breeding parameters.

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MALE-FEMALE DIFFERENCES IN PARENTAL CARE IN THE CRESTED AUKLET, A MONOGAMOUS SEABIRD

ABSTRACT

Differences in parental care between the sexes in ornamented species, may ultimately be the most important factor that is driving sexual selection, therefore to understand sexual variation may help us to further understand the mechanisms behind sexual selection. I studied patterns of parental care in Crested Auklets, a monogamous seabird, for three breeding seasons (1996 to 1998) in the Aleutian Islands, Alaska, using radio telemetry. In 1996, I found no sexual differences in parental care behaviours and low attendance rates, suggesting a poor food year. In 1997 and 1998, I found significant differences in parental care between males and females particularly early in the chick rearing period: males attended and brooded their single chick 47% more than females, while females provisioned 45% more than males. Overall, male attendance was positively correlated with female provisioning and attendance rates. I also found significant differences in prey types delivered to chicks between males and females for these two study years; males brought in 30% more euphausiids (larger prey items) whereas females brought in 36% more copepods (smaller prey items), however prey load size did not differ. In 1998, I measured how vulnerable young chicks were if left unattended using plasticine clay models placed in unoccupied crevices during three different time periods. Eighty-one to 87% of the models were attacked, with an average of 23 marks per model. I concluded that unattended crested auklet chicks appear vulnerable to attack. Male crested auklets have a larger and more strongly hooked bill and are more aggressive than females and I hypothesized that males are

better equipped than females to guard young chicks or the crevice nest site. While this bill shape difference probably evolved through intra-sexual selection, it has ecological consequences because male auklets preyed upon and delivered larger prey items than females.

INTRODUCTION

Patterns of male and female parental care vary widely among socially monogamous species. How and why individuals vary in the level of their care relates to several non-mutually exclusive factors. The amount of care provided by males may be determined by their confidence of paternity in their partner's offspring (e.g. Davies et al. 1992). When confidence of paternity is high and biparental care is required for offspring survival, such as in a socially monogamous seabird species, males invest heavily in parental care (e.g. Hunter et al. 1992), however variation in level of parental effort is still likely to occur between males and females. In some cases males and females invest differently because of inter-sexual differences in size or aggressiveness that affect their performance in the role of guarding offspring (e.g. Burger 1981). Individuals may also invest according to ecological constraints, such as food availability (e.g. Uttley 1992). Within species, individuals may invest according to their mate's breeding status (the "differential allocation hypothesis"; Burley 1986, 1988; deLope and Møller 1993). According to this hypothesis, individuals invest more with an attractive partner in parental care to maintain the pair bond. Further detailed

studies are required to explain the sources of variation in patterns of male and female parental care within and among monogamous species (Gowaty 1996).

Socially monogamous animals (monogamy defined as a "prolonged association and essentially exclusive mating relationship between one male and one female"; Wittenberger and Tilson 1980) offer some of the best opportunities to explore the causes and consequences of variation in parental care (defined as any behaviour by an adult that increases survival or fitness of their young; Clutton-Brock 1991) by males and females. Birds have been a classic group to investigate the relationship between parental care and monogamy, because within the broad definition of this concept 90% of bird species are monogamous (Lack 1968; Wittenberger and Tilson 1980) and thus offer wide opportunities to explore diversity of this mating system.

Biparental care is ubiquitous among seabirds, but it is of some interest as to how seabird pairs coordinate their activities, whether males and females adopt similar roles to achieve breeding success and how patterns of male-female parental care are related to ecological factors such as food abundance. Seabirds often live on isolated islands that offer protection from predators, but colony sites may be far from food resources (Ashmole and Ashmole 1967; Lack 1968). Within a breeding season both members of the pair care for the offspring, a behaviour that has enabled them to successfully rear young in an environment with patchy and unpredictable prey (Lack 1968). Studies quantifying inter-sexual variation of parental care in seabirds have demonstrated that males and females normally differ somewhat in their roles in rearing offspring (e.g.

Burger 1981; Gaston and Nettleship 1981; Montevecchi and Porter 1981; Creelman and Storey 1991). In a monogamous species with mutual mate choice both sexes should invest substantially in parental care (Trivers 1972; Andersson 1994), though *how* each sex invests may differ and be based on a variety of factors.

In this paper, I investigated patterns of parental care by females and males during the chick rearing period in a crevice nesting, ornamented seabird, the Crested Auklet (Jones 1993b). Crested Auklets are socially monogamous with low rates of extra-pair copulations (Hunter and Jones 1999) and both parents are required to successfully rear their single offspring each breeding season. Both sexes share incubation duties (approximately 35 days) and care for the single chick in a rock crevice until it departs the colony at about 35 days after hatching (Piatt et al. 1990; Chapter II). Differences in male and female attendance patterns at the colony in this species have been noticed but these have not been previously quantified (Fraser, Hunter and Jones, personal observation). This species is unusual among auks for the distinct sexual dimorphism in bill shape and size: males have a longer culmen and deeper bill than females and a hook at the bill tip (Jones 1993a; Gaston and Jones 1998 [illustration]). This bill dimorphism may be related to male intra-sexual aggression (Jones and Hunter 1999), but likely also has ecological consequences for foraging preferences and/or abilities (e.g. Bédard 1969a; Shine 1989).

In summary, the focus of my study was to elucidate the roles of male and female crested auklets in parental care. My specific objectives were to: 1) precisely quantify

the parental roles (provisioning and brooding of the chick) of male and female crested auklets using radio telemetry, 2) investigate how vulnerable young chicks are if left unattended in the nesting crevice and 3) analyze sexual differences in prey selection between males and females provisioning chicks. Prior to my study, little information was available on Crested Auklet parental attendance patterns.

METHODS

I studied Crested Auklets on Buldir Island (52° 21'N, 175° 56'E) in the Aleutian Islands, Alaska, USA, for three breeding seasons (1996 to 1998). Buldir, located in the western part of the island chain, provides habitat for one of the largest and most diverse seabird concentrations in the northern hemisphere (Sowls et al. 1978; Byrd and Day 1986). My study area on Buldir was located at "Main Talus", a colony with an estimated 250,000 Crested Auklets (Knudtson and Byrd 1982; Byrd et al. 1983).

Male and Female Provisioning and Attendance

Crested Auklets nest in rock crevices, therefore quantification of parental care was difficult and visual observations at nest sites were not possible. Therefore, to acquire data on attendance at nest sites I used radio telemetry. Transmitters (made by Biotrack and Holohil; frequencies ranged from 150.016 to 150.114, with pulse rates from 38 to 80 beats per min) were attached to steel leg bands (3.0 g; 1% of adult mass). I placed short range (< 5m) whip antennas at crevices, each connected to a Lotek (SRX 400) receiver by coaxial cables 25 to 60 m in length. The receiver was equipped with an

antenna switching device and a data logger recorded the presence of each bird in its crevice at three to five minute intervals (time interval was dependent on number of antennas that were running; pulse rates of transmitters and number of frequencies the receiver scanned). These records were stored on the data logger and downloaded every 48 hrs weather permitting. This system (powered by a set of solar panels and a battery) allowed me to continuously monitor individuals' activities at or near their nesting crevices 24 hours a day during the chick rearing period. Visual observations of birds tagged with transmitters entering and leaving crevices confirmed that antennas were picking up signals only when individuals were present within or next to their crevice.

Both pair members were captured after their chick hatched, sexed by bill shape, measured and tagged with individually identifiable radio transmitters and plastic color bands (1996: n = 7 pairs, 1997: n = 8 pairs, 1998: n = 6 pairs). Each record for an individual was classified as either: 1) a *feed* (provisioning) - when an individual was logged at its crevice after an absence of more than two hours (i.e. if a bird was not logged in for 20 minutes this was not considered a feed); a conservative estimate based on observations on our study plot and/or 2) *visit brood* (attendance)- when telemetry indicated that the adult was with the chick. In any one bout a bird could be assigned both a feed and visit if it stayed at the crevice for longer than one log-on (i.e. one log-on after a two-hour absence would be a feed, but more than one log-on after a two hour absence would be a feed plus the length of time the bird stays in crevice) . A

sample of these activities (e.g. time of arrival and whether the bird had food or not) were verified by direct visual observations of marked birds at crevices. Breeding individuals arriving at crevices after two or more hours of absence invariably had food in their throat pouches. No bird arrived earlier than two hours. Each member of a pair was assigned a behaviour regardless of their partner's behaviour, (e.g. if the pair spent the night in the crevice together, both were allocated time spent with the chick) and male and female pair behaviour were treated as independent in my analysis because the chick was often alone and there was evidence that pair members did not coordinate their activities (see Results).

I quantified provisioning (feeds/day/individual) and attendance rates (min/day/individual) for males and females. All parental activities were quantified in relation to chick age (see Chapter II for breeding chronology and chick aging methodology) and average rates of behavior among individuals were used in the analysis. I divided the chick rearing period up into two time periods chick ages 2 to 14 days and 15 to 25 days (hereafter referred to as early and late chick rearing) for three reasons: 1) coordination of parental activities was more critical in early chick rearing because of chick demands for brooding, 2) sexual differences of parental care activities were larger in early chick rearing and 3) there was variability in transmitter life (mean $\pm$ SD; 1996: 13.9 $\pm$ 3.8 days, n = 14; 1997: 27.7 $\pm$ 3.8 days, n = 16; 1998: 20.9 $\pm$ 7.7 days, n = 12). Most pairs were tagged with transmitters within the first week after the chick hatched. I also experimented with capturing adults during

incubation and tagged two males (their partners' were later tagged after the chick hatched) in 1997. Due to the variability of transmitter life all pair data (e.g. how much time a pair spent together) were based on how long the transmitters lasted within a pair.

I examined whether male and female provisioning and attendance rates were related to chick growth parameters (mass, wing length, age and date at fledging and linear growth of mass and wing; see Chapter II for chick growth methodology) and whether provisioning and attendance were related within each sex, between males and females and within each study year. I also compared how much time a pair spent together at their crevice between years, as a possible indicator of food within a breeding season. Condition measured as mass regressed on tarsus (Jones and Montgomerie 1992) was estimated and examined in relationship to parental effort (provisioning and attendance) and chick growth quality (limited to hatch date, fledging mass and fledging wing).

Chick Vulnerability

In 1998 I measured how vulnerable a young unattended chick was, by placing realistic plasticine model chicks (made of gray or brown plasticine and equipped with black glass eyes, an artificial bill and black 'down' made from yarn; approximately 6 cm high by 10 cm long, similar to a five day old chick) in previously occupied Crested Auklet crevices, (i.e. unoccupied during the 1998 breeding season). Thirty-one models were placed out for five day intervals, in the same crevices, during three different time periods: 1) pre-hatching (25 June to 30 June), 2) early chick rearing (7

July to 13 July) and 3) mid-chick rearing (21 July to 26 July). At the end of each trial the models were collected and the number of bill marks (pokes, scrapes and bites) from Crested Auklets and other auk species were recorded. I also collected bill marks on plasticine from captured birds of Crested and Least (*A. pusilla*) Auklets and from Horned Puffins (*Fratercula corniculata*).

Male and Female Prey Selection for Chick Provisioning

To quantify sexual differences in selection of prey delivered to chicks I collected food samples from male and female Crested Auklets during 1996 to 1998. Crested Auklets prey on zooplankton, predominately euphausiids and copepods (Bèdard 1969b) and chick meals are carried in a sublingual pouch (Piatt et al. 1990). Adults were captured on our study plot as they arrived at the colony (using noose carpets) and the contents of their sublingual pouches were collected. Afterwards each bird was measured, sexed, banded and released. I estimated the percent of the food load that was collected (some food was invariably lost in the cracks of rocks), weighed the fresh sample and preserved it in 70% ethanol. To quantify prey selection, all taxa except euphausiids were counted and average masses were obtained. Euphausiid mass was calculated by subtracting the mass of the counted species from the total fresh mass. In the majority of the food samples collected, I was unable to either identify euphausiids to genus or count them because few of them were whole and most were broken down into small pieces (head and tail were missing and presumably came off when the euphausiid was captured). I used a Mann-Whitney test on aggregated percent of mass

('the average contribution of a prey type within each sample'; Duffy and Jackson 1986, Swanson et al. 1974) within each year, for each species, to test for differences between males and females.

RESULTS

Incubation and Abandonment

In 1997, I captured 15 adults (at night to help minimize the likelihood of abandonment): three pairs, seven males and two females during incubation and found them to be highly susceptible to disturbance at this stage. All of the crevices in which a female was handled failed. Of the males captured alone (i.e. partner not captured, n = 7) only one abandoned (86% success). In the crevices in which both members of the pair were captured, males were subsequently observed incubating, but the females were not: all three of these pairs failed prior to hatching. I also tested whether there were differences between years in the likelihood of abandonment after handling an adult during the early part of chick rearing and found that 1996 (48% abandoned after handling) had a higher percentage of abandonment than did 1997 (17%) or 1998 (14%; χ^2 = 6.3, df = 2, P = 0.04; *post hoc* cell contributions for crevices that failed: 1996 = 2.5, 1997 = -1.1, 1998 = -1.4).

In 1997, I radio tagged two males during incubation 10 and 14 days prior to hatching (their partner's were tagged after hatching). While I could not tell whether there was pair overlap (rarely were pairs together during the day, but sometimes pairs were

observed in their crevice together at night) I was able to record male presence/absence at the crevice. For the first male, presence at the crevice ranged from 12 to 78 hours and absence from 12 to 36 hours. The second male presence's ranged from 6 to 21 hours and absence from 6 to 50 hours. No discernible periodic incubation pattern could be detected from these two birds.

Male and Female Chick Provisioning and Attendance

I tagged a total of 21 different pairs of Crested Auklets with transmitters during early chick rearing during the three study years. Birds did not appear to be adversely affected by the presence of the transmitter and engaged in normal activities such as courting on the colony site surface. Of the 14 times I visually observed radio tagged birds arriving at their crevice, in all cases the bird had an obvious food load as indicated by a swollen throat pouch. Therefore, I assumed that every time an individual arrived at its crevice (using the criteria stated above) that it had food. I am confident that the provisioning rates and attendance telemetry data are realistic of activity at the crevice from our observations. For example, I observed one male, arriving with food at 1111 h (7 Jul 1997) just outside his crevice. This male's last reading was on 0829 h the same day and he was not read again until the exact time we observed him by his crevice. I obtained readings like this for 13 of the 14 birds that were observed arriving with food. Overall, the majority of birds arriving at the colony (from plot observations) carrying food immediately went underground. Crested Auklets were vulnerable to predation and kleptoparasitism by Glaucous-winged Gulls

(*Larus glaucescens*) who killed arriving auklets and consumed lost food loads.

I analyzed parental effort using a three-way ANOVA model (type III) that included sex, year and chick age (early and late). Rates of attendance varied between sexes, among years and chick age, there was also a significant interaction between sex and chick age (ANOVA, year, F = 113.3, df = 2 and 120, P <0.0001; sex, F= 40.2, df = 1 and 120, P < 0.0001; chick age, F = 86.4, df = 1 and 120, P <0.0001; year * sex, F = 18.3, df = 2 and 120, P < 0.0001; sex * chick age, F = 5.8, df = 1 and 120, P < 0.02; Table 3.1). There was significant differences among all years in rates of attendance as well as between sexes and chick age (Fisher's PLSD: 1996 vs 1997, P < 0.0001; 1996 vs 1998, P = 0.01 and 1997 vs 1998, P < 0.0001 male vs female, P < 0.0001 and chick age, P < 0.0001). In 1997 and 1998 males attended their chick 47% more than females, whereas in 1996 I found no sexual differences in attendance.

Rates of provisioning also varied between sexes and among years and there was a significant interaction between sex and chick age (ANOVA, year, F = 10.9, df = 2 and 128, P <0.0001; sex, F= 4.8, df = 1 and 128, P = 0.03; chick age, F = 0.07, df = 1 and 128, P =0.8; year * sex, F = 3.2, df = 2 and 128, P = 0.04; sex * chick age, F = 19.3, df = 1 and 128, P < 0.0001; Table 3.2). *Post hoc* tests revealed significant differences in provisioning rates between 1996 and the other two study years and a mean difference of provisioning between males and females (Fisher's PLSD: 1996 vs 1997, P < 0.0007; 1996 vs 1998, P < 0.0001 and 1997 vs 1998, P < 0.3; male vs female, P < 0.02). In 1997 and 1998 females provisioned their chick 45% more than

Table 3.1. Provisioning rates of male and female Crested Auklets at Buldir Island, Alaska.

	feeds/day/individual					
	Male (SD)			Female (SD)		
	early[a]	late	total	early	late	total
1996	1.3 (0.5)	1.4 (0.6)	1.4 (0.6)	1.4 (0.3)	1.1 (0.3)	1.3 (0.3)
1997	1.3 (0.3)	1.6 (0.3)	1.4 (0.3)	1.8 (0.3)	1.6 (0.4)	1.8 (0.4)
1998	1.3 (0.5)	1.8 (0.4)	1.6 (0.5)	1.9 (0.2)	1.7 (0.4)	1.8 (0.3)

[a]Chick age, early (1-14 days) and late (15-25 days).

Table 3.2. Attendance rates of male and female Crested Auklets at Buldir Island, Alaska

	minutes at crevice/day/individual					
	Male (SD)			Female (SD)		
	early[a]	late	total	early	late	total
1996	216 (141.2)	26 (10.6)	153 (146.3)	213 (130.7)	58 (48.6)	154 (130.5)
1997	850 (144.1)	494 (214.6)	693 (251.1)	451 (103.8)	264 (131.0)	365 (148.9)
1998	398 (155.2)	166 (67.7)	287 (167.6)	219 (71.9)	102 (66.8)	160 (90.6)

[a]Chick age, early (1 - 14 days) and late (15 -25 days)

males early in chick rearing, while in 1996 I found no sexual differences in provisioning.

I found that female provisioning and attendance rates were each positively correlated between early chick rearing and late chick rearing and females that provisioned more also attended more late in chick rearing (Table 3.3). Male attendance was positively correlated between early and late chick rearing. Overall years, male attendance was positively correlated with total female provisioning and attendance (Table 3.4).

Male condition (residuals from mass regressed onto tarsus) was positively related to early chick attendance (r = 0.48, P = 0.03), but not to provisioning (r = -0.3, P = 0.11). No significant relationships were found for the selected chick growth variables (hatch date rank: r = 0.05, P = 0.8, fledging mass, r = 0.11, P = 0.5; fledging wing r = -0.01, P = 0.9). Female condition was significantly related to early chick provisioning (r = -0.48, P = 0.03), but not to attendance (r = 0.07, P = 0.8). Chick fledging mass (r = 0.4, P = 0.01) was significantly related to female condition, however hatch date rank (r = -0.2, P = 0.3) and fledging wing (r = 0.17, P = 0.3) were not.

I found no differences in linear growth or fledging parameters between chicks with parents fitted with transmitters and those without transmitters (Mann-Whitney U tests, all $P > 0.05$). The amount of time a chick was left unattended varied considerably among pairs and years and increased as the chick got older ($\bar{x} \pm$ SD, $\bar{x}_{week\ 1}$ = 12.8 $\pm$ 5.1; $\bar{x}_{week\ 2}$ = 15.7 $\pm$ 6.4; $\bar{x}_{week\ 3}$ = 18.9 $\pm$ 6.6 hr/day).

Table 3.3. Relationships between chick provisioning and attendance for Crested Auklets.

	females *n* = 21	males *n* = 18
Provisioning: E&L[a]	0.46*	0.25
Attendance: E&L	0.69**	0.87**
Early chick: Prov & Atten[b]	0.2	-0.36
Late chick: Prov & Atten	0.44*	-0.3

[a]E=early, L=late chick rearing.

[b]Prov=provisioning, Atten=attendance.

* $P < 0.05$, ** $P < 0.001$, Spearman Rank correlations.

Table 3.4. Relationships between male and female chick provisioning and attendance rates (years combined) for Crested Auklets from 1996 to 1998.

	male					
	prov-E	prov-L	atten-E	atten-L	prov-total	atten-total
female						
prov-E[a]	-0.13	0.29	-0.43	-0.31	--	--
prov-L[b]	-0.07	0.23	0.37	0.4	--	--
atten-E[c]	-0.18	0.03	-0.17	-0.08	--	--
atten-L[d]	-0.18	0.31	0.72*	0.67*	--	--
prov-total[e]	--	--	--	--	-0.02	0.39*
atten-total[f]	--	--	--	--	-0.04	0.73*

[a]prov E=provisioning early (chick age 1 to 14), [b]prov-L -provisioning late (chick age 15 to 25).
[c]atten-E -attendance early (chick age 1 to 14), [d]atten-L - attendance late (chick age 15 to 25).
[e]prov-total -total rates of attendance (chick age 1 to 25), [f]atten-total - total rates of attendance (chick age 1 to 25).
* $P < 0.05$, Spearman rank correlations.

There was a significant relationship between female attendance and linear growth of wing (correlation matrix, $r = 0.88$, $P_{female} < 0.01$). Other chick growth parameters fledging age, fledging mass, fledging date, and linear growth of mass were not related to male or female attendance (correlations, Ps > 0.05). Nor were male and female provisioning rates related to any of the chick growth parameters (Ps > 0.05).

The amount of time a pair spent together in their crevice was highly variable. I found significant differences in the amount of time a pair spent together among years with males and females spending very little time together in 1996 ($\bar{x} \pm$ SD, $\bar{x}_{1996} = 25.3 \pm 34.3$; $\bar{x}_{1997} = 332.3 \pm 288.0$; $\bar{x}_{1998} = 107.8 \pm 81.5$ min/day/pair; $F = 9.9$, df = 2 and 20, $P = 0.001$; pairwise comparisons, Tukey's test 1996 vs 1997, $P < 0.05$; 1996 vs 1998, $P > 0.05$ and 1997 vs 1998, $P < 0.05$). In 1997 (the season in which the transmitters lasted the longest), I examined the amount of time a pair spent together over the chick rearing period (weeks two to four) and found that it declined as the season progressed ($\bar{x} \pm$ SD; $\bar{x}_{week\ two} = 303.5 \pm 206.7$; $\bar{x}_{week\ three} = 204.8 \pm 120.8$; $\bar{x}_{week\ four} = 71.6 \pm 40.4$ min/day/pair; repeated measures ANOVA, $F = 4.14$, df = 2 and 20, $P = 0.03$).

The consistent pattern of male and female parental care during early chick-rearing was particularly striking (Figs. 3.1 and 3.2). If a female spent the night in the crevice 89 $\pm$ 14.2 % (mean calculated on a per female basis, years combined $\pm$ SD, early chick rearing) and 98 $\pm$ 8.8% (late chick rearing) of the time she left the colony between 0500 and 0730 and would usually return sometime during the morning

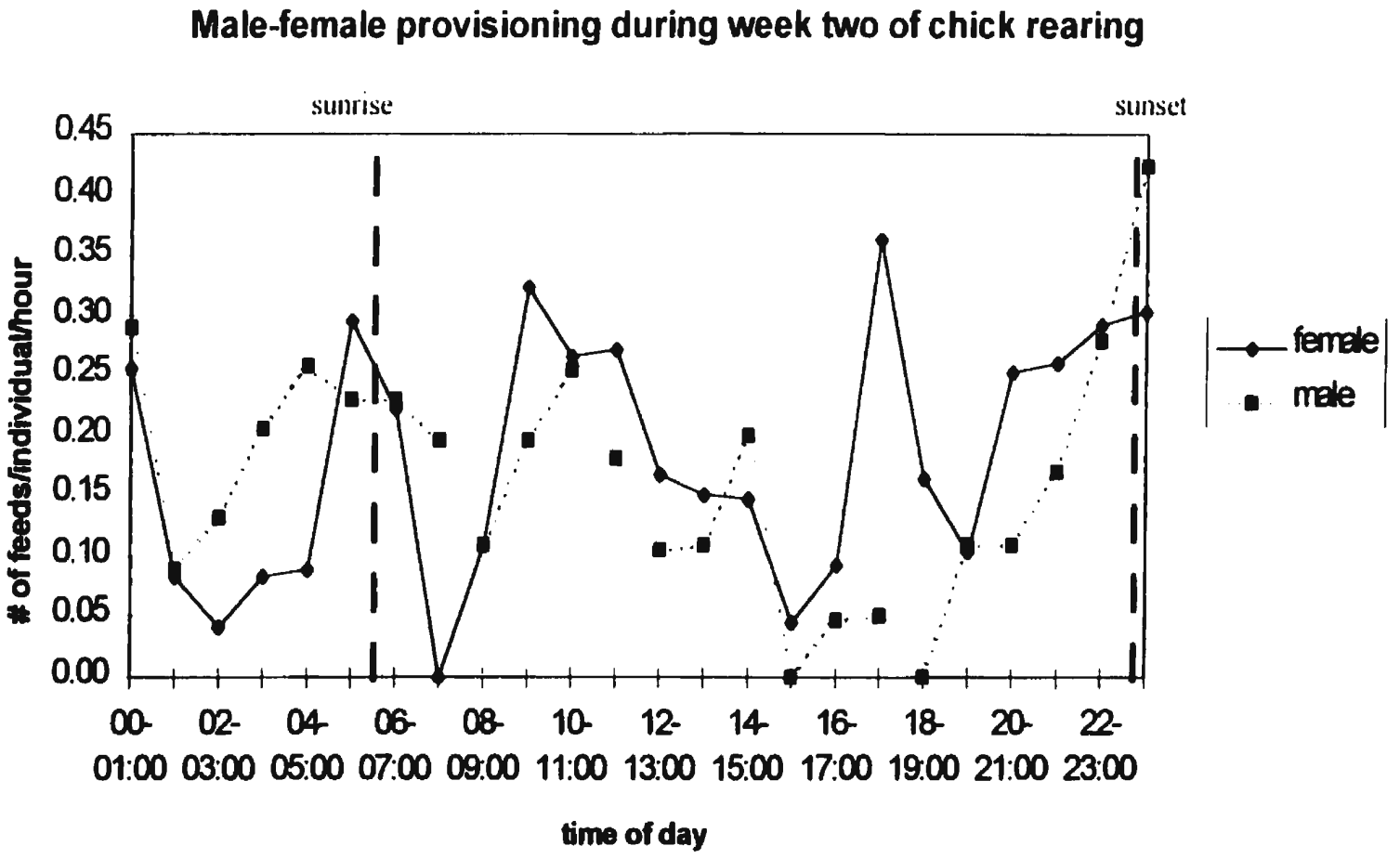

Figure 3.1. Patterns of provisioning by male and female Crested Auklets during week two of chick rearing

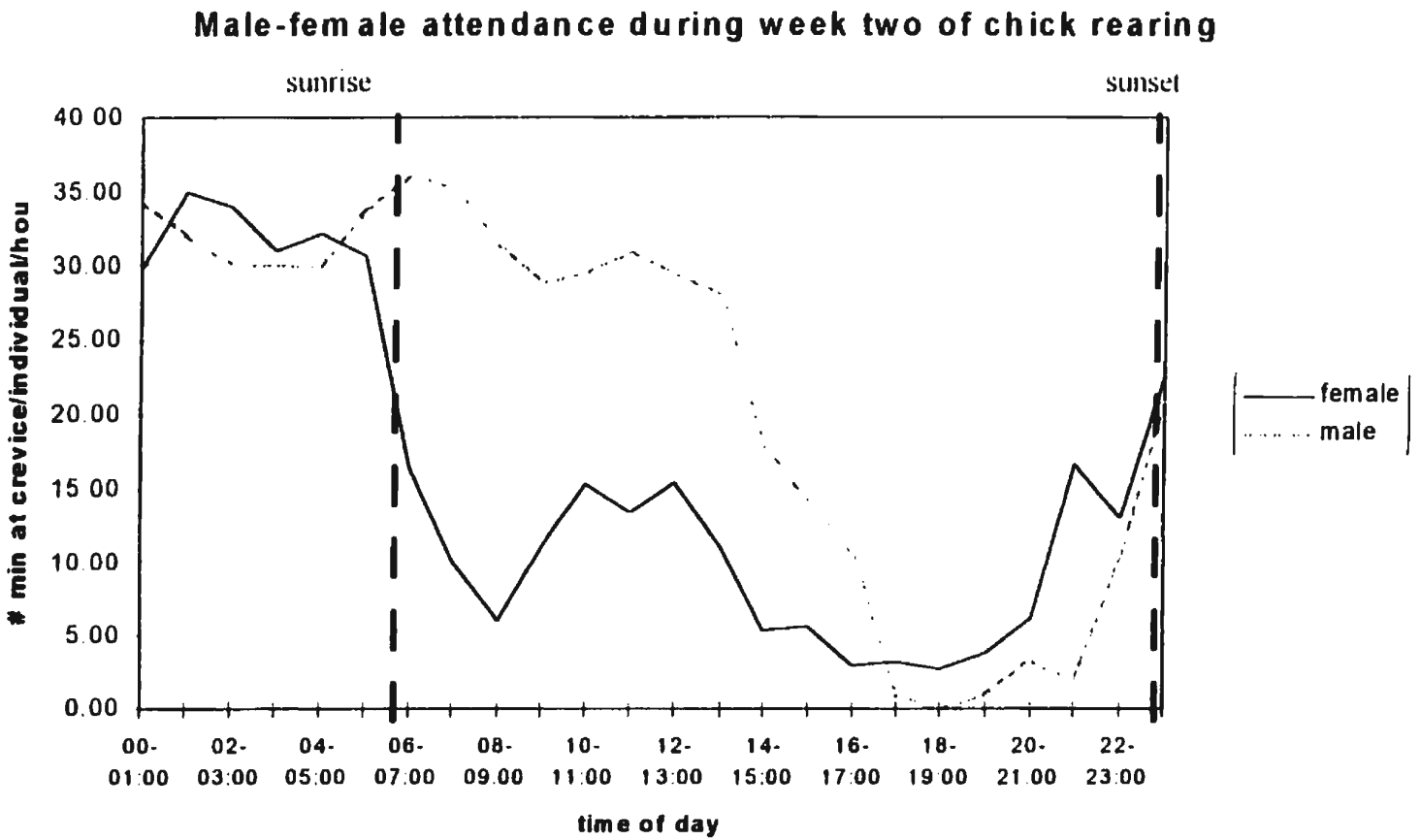

Figure 3.2. Patterns of attendance by male and female Crested Auklets during week two of chick rearing.

activity period (1000 to 1400) and/or in the early evening (1800 to 2100). On the other hand, if a male spent the night in the crevice 88 ± 12.1% (early chick rearing) of the time he stayed with the chick throughout the morning and early afternoon (i.e. did not leave the colony in the early morning). However, this pattern changed markedly for males and decreased to 26 ± 37.7% in late chick rearing.

I examined whether males and females were more likely to provision during different times of the day in early and late chick rearing. The two activity periods provided the basis for dividing the day into four time periods (0000 to 0600; 0600 to 1200, 1200 to 1800, 1800 to 2400). On a per female/male basis, overall sexual differences in food provisioning were not significantly related to time of day for either early or late chick rearing (early: $X^2 = 5.3$, df = 3; $P < 0.15$; late: $X^2 = 1.2$, df = 3; $P = 0.8$). However, females came in more often during the early evening (1800 to 2100) than did males (77% greater frequency; see Fig. 3.1) and this difference was masked when the data was divided into six hour time periods (and there were not enough data to divide the day into 3 hour periods).

Chick Vulnerability

Young chicks left unattended appeared to be quite vulnerable to attacks. Throughout my study I found three dead chicks that had injuries consistent with having been attacked by an adult (i.e. with peck marks breaking the skin and evidence of trampling). Also, the dead chicks were all small; less than one week old. In trials one (prehatching) and two (peak hatching) of the model clay experiment, 81% of the

models were marked and in trial three 87%. There was a significant difference in the number of marks (pokes, scrapes and bites) that the models incurred during each trial ($\bar{x} \pm$ SD; $\bar{x}_{\text{trial one}} = 19.4 \pm 24.5$; $\bar{x}_{\text{trial two}} = 11.9 \pm 18.1$; $\bar{x}_{\text{trial three}} = 36.8 \pm 38.2$; repeated measures ANOVA, $F = 9.57$, df = 2 and 31, $P = 0.0002$). The body and head of the models were equally likely to have marks ($t = 1.53$, df = 60 and 31, $P = 0.13$). Most of the marks on the models were pokes or scrapes, which were most likely from Crested Auklets, as these matched marks obtained from Crested Auklets captured on the study plot, however in three instances the bites on the models much bigger and were likely to have been delivered by a puffin. I also had one chick model completely disappear, which I presume to have been taken by a puffin.

Male and Female Prey Selection for Chick Provisioning

Males and females provisioned chicks with food loads of similar mass, and the mass of the load increased later in the chick rearing season ($\bar{x} \pm$ SD; $\bar{x}_{\text{female}} = 8.1 \pm 4.7$ g, $n = 155$, $\bar{x}_{\text{male}} = 9.3 \pm 5.9$ g, $n = 85$; $\bar{x}_{\text{early}} = 9.6 \pm 5.6$ g, $n = 155$; $\bar{x}_{\text{late}} = 11.8 \pm 6.1$; Two-Way ANOVA: sex: $F = 0.4$, df = 1 and 236, $P = 0.21$; chick age: $F = 8.6$, df = 1 and 236, $P = 0.003$; sex * season $F = 0.9$, df = 1 and 236, $P = 0.3$). Crested Auklets brought in four main prey items: euphausiids, two species of copepods *(Neocalanus cristatus, N. plumchrus)* and the Hyperiid amphipod, *Parathemisto pacifica*. I found significant differences between males and females in 1997 and 1998 in their selection of prey items (Table 3.5). Males brought in higher proportions of euphausiids than females, whereas females brought in higher proportions of copepods

Table 3.5. Mean aggregate percent mass composition of chick food loads for male and female Crested Auklets from 1996 to 1998.

	1996			1997			1998		
percent prey:	male	female	*P* (*U*)	male	female	*P* (*U*)	male	female	*P* (*U*)
euphausiids	78.2	79.3	0.7 (500)	68.8	49.2	0.04 (469)	63.4	42.3	0.0006 (545)
Neocalanus cristatus	16.7	16.3	0.94 (523)	28.3	39.6	0.05 (470)	35.0	56.0	0.0008 (553)
N. plumchrus	1.1	2.8	0.5 (475)	5.1	11.7	0.03 (448)	1.0	1.7	0.93 (969)
Parathemisto pacifica	0.19	0.3	0.62 (490)	1.2	1.6	0.23 (539)	0.6	0.5	0.98 (977)
other	7.5	2.8	0.94 (523)	0.7	0.3	0.64 (602)	0.03	0.2	0.42 (878)

Other category included: crab megalopa, crab zoea, shrimp zoea, larval fish, pteropods, and snails.

in 1997 and 1998. In 1996 there was no difference between the sexes in the proportions of each type of prey brought in.

DISCUSSION

Male and Female Chick Provisioning and Attendance

For two of my three study years I found male and female Crested Auklets to have distinct roles in parental effort, particularly during the early part of the chick rearing period. Males stayed with the chick more, while females fed the chick at higher frequencies. While division of labor existed in two of the study years, total male attendance and female provisioning and attendance were positively related; increased rates of provisioning did not result in less chick attendance (Table 3.4). Male and female feeding and attendance rates were not predictive of most chick growth parameters, though female attendance rates predicted the rate of linear growth of wing, which is an important factor that influences chick survival (Chapter II).

So the question arises, why did males spend more time with small chicks than females? I hypothesized that chicks needed protection from conspecifics and puffins and because males are more aggressive in agonistic interactions than females (Jones and Hunter 1999) and have larger and stronger bills (Jones 1993a), they would be better at guarding their chick from prospecting individuals. Although Crested Auklet chicks develop homeothermic abilities four to five days post hatching (Jones 1993b; personal observation), it appears that they require further guarding past this stage. If

the model chicks were representative of unattended chicks, our experiment indicated that chicks left alone were highly vulnerable to attacks and that the likelihood of attacks increased after peak hatching. This was supported by my findings of chicks that had been pecked to death in their natal crevices, presumably in the absence of a defending parent. However, Crested Auklet males may also be defending the nest site because males usually retain the crevice from year to year (Chapter VI). Similarly, Creelman and Storey (1991) also concluded this for Atlantic Puffins (*Fratercula arctica*).

Many pairs fail during peak hatching and there is an influx of individuals at the colony engaged in courtship activities and prospecting for future partners and nest sites. Attendance would therefore be critical when chicks are small and less mobile, especially during the activity periods when peak numbers of conspecific failed breeders and prospectors are present at the colony. Indeed, this is the time when I observed males most likely to be with their chick in their crevice. If chicks required attendance only for thermoregulation, then attendance would drop off quickly, which does not appear to be the case. In years when food is low or harder to come by, parents must make the decision to guard their chick or to leave it unattended to find food, but it is possible that in these years prospecting birds are at in low numbers and the risk of attack is lower.

Subtle male-female differences in parental care appear to be the norm rather than the exception for seabirds even though in all species both sexes contribute substantially

(e.g. Burger 1981; Gaston and Nettleship 1981; Montevecchi and Porter 1980; Wanless and Harris 1986; Creelman and Storey 1991). For example, Black Skimmer (*Rynchops niger*), Guillemot (*Uria aalge*) and Atlantic Puffin females fed their chick more, while males engaged more in maintaining and defending the nest site (Burger 1981; Wanless and Harris 1986; Creelman and Storey 1991). On the other hand, while Montevecchi and Porter (1980) found that Northern Gannet (*Morus bassanus*) males fed their chick more when it was young, while females fed the chick more when it was older, males still contributed more in the establishment and possession of nest sites. Also, in many of these species males are larger than females, which presumably relates to levels of aggression (e.g. Black Skimmers, Atlantic Puffins and Razorbills; Burger 1981, Creelman and Storey 1991, Wagner 1999).

Thus, sexual differences in parental care duties may be attributed, proximately, to the different levels of aggression between males and females and the level of such differences may be influenced by ecological factors such as weather conditions and food availability. For example, Uttley (1992) attributed male-female differences in patterns of attendance to food availability in an inter-colony comparison of breeding Arctic Terns (*Sterna paradisaea*). The variation in attendance rates and female provisioning rates among years that I observed in my study may have been related to changes in prey abundance as suggested by higher provisioning and attendance rates in 1997 and 1998.

Male and Female Prey Selection for Chick Provisioning

In 1996, I found no male-female differences in provisioning or attendance rates, or for prey selection, so why was 1996 different to the other study years in terms of male-female parental care? I observed lower feeding and attendance rates, low occurrences of mates paired at their crevice, lower breeding success, lower adult mass and a higher likelihood of abandonment after handling (Chapter II; this study). The percentage of copepods brought in was significantly lower and the percentage of euphausiids significantly higher in 1996 compared to the other two study years (Table 3.5) Larger prey items, like euphausiids, should be preferred by both males and females because they are, presumably, more efficient in terms of energy intake gained per unit effort catching prey. One possible scenario is that females prefer to collect the larger (euphausiid) prey but they can't because they are physically constrained, possibly by their smaller bill and/or by body size. Females may simply have a harder time handling larger prey items like euphausiids and/or they may have to expend more energy in a foraging bout than males (because they are smaller in body size and mass) to catch fast swimming euphausiids. Males may take euphausiids because their larger bill and body size allows them to take them (*Thysanoessa* up to 32 mm; Newell and Newell 1977) more efficiently and they may also have a harder time catching copepods because of the hook at the end of their bill. Therefore, females may catch small prey like copepods (*N. cristatus*, 4.9 - 8.9 mm; *N. plumchrus*, 3.4 - 5.2 mm; Gardner and Szabo 1982) because it is more efficient to do so.

In 1996, if euphausiids were smaller and there were fewer copepods, females may

have ended up with a higher proportion of euphausiids in their diet than in other years because they came within the size range that females could take. Though females may still have had to work harder to bring in euphausiids in a year when copepods were scarce and this may explain why only females appeared to have lower feeding rates in 1996. However, prey availability probably affected both males and females in 1996, as indicated in lower attendance rates and higher amounts of alternative prey items in the diet of both sexes. In addition, Least Auklets (*A. pusilla*), which preferentially prey on copepods (Bédard 1969b; Hunt and Harrison 1990; Hunt et al. 1990), had an unusually low survival rate over the winter of 1995 to 1996 (Jones and Hunter unpublished data), also consistent with a shortage of copepods in that year. Least and Whiskered Auklets (*A. pygmaea*) also had higher percentages of euphausiids in their diet that year (Fraser, Williams, Jones and Hunter unpublished data) which suggests that euphausiids were smaller.

Bedard (1969b) found no evidence that male and female auklets selected different prey during incubation and chick rearing from St. Lawrence Island. However, my study has shown sexual differences in the proportion of prey selected during the chick rearing period. It is possible that these behavioral differences are specific to my study site (and possibly to other colonies on Buldir) due to the unique, physiographic features surrounding the island (Springer et al. 1996), however further knowledge of zooplankton distributions around Buldir is required. A study that incorporated inter-colony/island comparisons would allow further investigation between the relationship

of sexual variation in prey selection and local oceanographic features around different colonies. Also, if differences in male and female behaviour are influenced by ecological factors (Uttley 1992), inter-colony/island differences would be expected.

Male-female differences in prey selection and foraging strategies have been noted in other seabirds. For example, Weimerskirch et al. (1997) found that female wandering albatross (*Diomedea exulans)* were more likely to bring their chick oceanic prey species, whereas males were more likely to bring prey from the shelf edge and males contributed 50% more energy than females towards the chick. It is possible that the patterns observed of male-female chick provisioning in Crested Auklets may result in similar differences in energetic investment. However, food load size delivered by male and female Crested Auklets did not differ significantly, and according to data summarized by Bèdard (1969b), copepods and euphausiids have similar nutritional content.

Three theories exist to explain the development of morphological differences in trophic structures between males and females within a species: intra-sexual selection, sexual conflict (Gowaty 1996) and ecological niche divergence (Shine 1989). Gowaty (1996) emphasized that whenever males and females are in conflict over various aspects of reproduction provides the grounds for selection on males to manipulate females. Male control of the crevice could certainly be viewed as male resource brokering, however I require further evidence on pre-incubation crevice attendance to distinguish between intra-sexual selection and sexual conflict. Shine (1989) noted if a

trophic structure was used in sexual interactions, breeding was seasonal, and seasonal variation of the structure existed, than intra-sexual selection was probably the mechanism involved in its evolution. Crested Auklet males engaged in intra-sexual interactions during mate choice activities in which they frequently used their bill in an aggressive manner towards other males (Jones and Hunter 1999), they appeared to be flexible in prey choice during the chick rearing period (Bèdard 1969b) and their bill plates are shed every season and are only replaced for the breeding season. Thus, it seems likely that differences in Crested Auklet bill shape have probably developed from intra-sexual selection in males through chick and/or nest site protection or competition for mates (Jones 1993b; Jones and Hunter 1999; Chapter IV) and that the development of a larger, deeper bill has allowed them to be better equipped for chick protection than females.

In a monogamous seabird that engages in mutual mate choice (Jones and Hunter 1993; Jones and Hunter 1999), such as the Crested Auklet, equal care from each member of the pair would be expected. However, because males and females have different physiological constraints and needs and confidence of parentage, there should be no reason to expect identical behaviour in offspring investment. Comparisons of the costs incurred from the different behaviours of male and female Crested Auklets are difficult. One way to identify whether the costs of different investment patterns vary greatly would be to examine survival rates. Because females fed their chicks more frequently, I predicted lower survival rates due to increased vulnerability from

predators in movement to and from the colony. However, there are no sexual differences in survival rates of this species at Buldir (Jones and Hunter unpublished data). Therefore the costs that males may incur related to remaining at the colony more are: 1) long-term negative effects of higher testosterone levels associated with agonistic interactions, 2) increased risk of injury due to agonistic interactions with conspecifics or other species such as puffins and 3) more stress from going for longer bouts without food while chick guarding.

Conclusions

My results are consistent with there being a fundamental relationship between parental care and sexual selection in this socially monogamous seabird. Based on my findings, I hypothesized a chain of events linking these phenomena. I believe intra-sexual selection on male characteristics related to competition for mates or nest sites initially produced sexual dimorphism in bill shape and body size in this species. An indirect effect of this was differences in prey selection, since larger billed/heavier males would then have been predisposed to feed on larger prey (euphausiids) than the smaller billed females (copepods). At the same time, intra-sexually selected male aggressiveness would have produced a situation in which small chicks were vulnerable to prospecting non-breeding/failed breeder males, creating the need for male parents to remain in the nesting crevice to protect their chick. Female parents would then be free to invest more heavily in chick provisioning early in chick development. Later in the season, both sexes provision the chick, which at this stage of development would be

less vulnerable to attack by other auks. This explanation for patterns in parental care has several testable predictions: 1) no other auk species has this dichotomy in aggressiveness and bill shape, so in other auk species which lack inter-sexual differences in aggressiveness and bill shape there should be few or no differences in parental care behaviour between the sexes, 2) closer examination of male and female prey selection for chick provisioning at colonies other than Buldir should show a similar pattern of male-female differences if prey is of similar size and proportional distribution to that at Buldir; 3) Crested Auklet foraging for self maintenance (not related to chick rearing) should parallel what we found for chick provisioning, and there should be greater inter-sexual differences in prey selection during the summer, when bill shape is most different, compared to winter.

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ORNAMENTATION, PARENTAL EFFORT AND MATE RETENTION IN A MONOGAMOUS SEABIRD, THE CRESTED AUKLET

ABSTRACT

I quantified the relationship of a sexually selected ornament to parental effort and mate retention in a socially monogamous seabird, the Crested Auklet. I examined crest length (absolute length of own and partner's) and provisioning and attendance during early chick rearing using radio telemetry (n = 21 pairs). Using simple game theory models we examined whether crest length was an advertisement of a direct benefit-ability to provide parental care or whether crest length was indicative of an indirect benefit. If crest length was a direct benefit, the prediction was a positive relationship between crest length and parental care. If crest length is an indirect benefit then a negative relationship between length and parental care should occur as well as differential allocation of parental care within the pair according to mate attractiveness. Male attendance and provisioning were not related to their own crest length, however males increased provisioning rates according to their partner's crest length. Female attendance was positively related to their partner's crest length. Female crest length was negatively related to provisioning rates. These results supports the prediction that crest length is an advertisement of an indirect benefit. Mate retention was related only to female crest length; shorter crested females were more likely to split. Males kept the crevice nest site if a pair split and were more likely to pair with a longer crested female. Based on mate retention patterns and differential allocation of parental effort, it appears that male Crested Auklets may have more control over remating decisions and mutual sexual selection may be more biased towards males.

INTRODUCTION

Møller and Thornhill (1998) recently investigated the relationship between secondary sexual ornaments and the extent of male parental care on the basis of whether ornaments used in mate choice provided information on direct or indirect benefits to the chooser. They predicted that in species in which the ornament reflects a direct benefit to the chooser, attractive males should provide extensive parental care and no differential investment in offspring should occur on the basis of this attractiveness (prediction #1). In species in which the ornament reflects attractiveness (an indirect benefit such as good genes), more ornamented males should provide relatively less parental care than their mates and females relatively more (prediction #2). Differential allocation to offspring according to mate attractiveness was initially developed by Burley (differential allocation hypothesis-DAH; 1986). DAH predicts differential investment according to mate attractiveness because females mated to highly attractive males produce sexy sons who have a higher reproductive success (Burley 1986). However, the differential allocation hypothesis has only been investigated from the female's perspective of her mate's attractiveness (Burley 1986, 1988; deLope and Møller 1993; Rohde et al. 1999).

Do the above predictions also hold in species with obligate biparental care in which both males and females actively choose partners based on sexual displays of ornaments? If an ornament reliably reflects a direct benefit to the choosers, then no differential investment should occur by either sex on *the basis of mate preference for*

an ornament. If an ornament reflects only mate attractiveness or viability (i.e. an indirect benefit) would we predict differential investment occurring by both the male and female? Should males differentially invest when paired with an attractive mate to produce attractive daughters? Male investment in offspring may depend on his confidence of paternity and therefore differential investment may depend on his own attractiveness. In this paper I examine the two predictions for both males and females using a game theory model in which the four players are attractive males, attractive females, unattractive males and unattractive females (Tables 4.1 and 4.2).

The two models yield the same outcome when pairs are similar in ornamentation (i.e. attractive males+attractive females and unattractive males+unattractive females). However, when a difference in attractiveness within the pair exists, the two models yield different outcomes. The key to investigating the outcomes in model #1 is related to what is identified as a direct benefit. In this scenario the *only* direct benefit we test is the ability of individuals to provide parental care. There may be other direct benefits that are related to the degree of ornamentation, such as territory size or greater fertilization success, however neither of these direct benefits predict differential parental expenditure and therefore they are not considered here.

In model #1, the ornament advertises the ability to provide parental care. The predicted outcome for when an 'attractive' male is paired with an 'unattractive' female is that male parental expenditure (PE) will be greater than female PE and when an 'unattractive' male is mated to an 'attractive' female, than the female should have a

higher rate of PE (Table 4.1). If the ornament is not related to PE at all, but rather signals attractiveness (model #2), an indirect benefit, then the outcomes for the two pairing are different (Table 4.2) and we must consider the DAH (Burley 1986).

If an 'attractive' male is paired with an 'unattractive' female, then female PE will be greater than male's because she would be willing to invest more in offspring to keep her attractive partner (Table 4.2). If an 'unattractive' male is mated to an 'attractive' female, then the male should have a higher rate of PE. However, whenever an 'attractive' female is mated to an 'unattractive' male and attractiveness is related to an indirect benefit like good genes, then we must also predict that females will try to obtain extra-pair fertilizations (EPFs). If females mated to unattractive males obtain EPFs then the outcome would be reversed and female PE should be greater than or equal to her social partner. The outcome of both of these models rests upon the assumption that the ornament conveys the same information to both males and females.

In this paper I compare the predictions from two models of ornamentation as they relate to PE in Crested Auklets. Crested Auklets are a socially monogamous seabird with obligate biparental care. Both males and females possess a crest that varies in size among individuals and is displayed during courtship activities throughout the breeding season (Jones 1993b; Jones et al. 1999). The variation in crest length has been the focus of some mate preference experiments (Jones and Hunter 1993, 1999). Both male and female Crested Auklets approached longer crested models more closely

Table 4.1. Predictions of outcomes for parental expenditure (PE) if ornament (crest) indicates parental care abilities (i.e. direct benefit).

	'attractive' male= good parent	'unattractive' male=poor parent
'attractive' female= good parent	male PE = female PE	positive relationship between crest length and PE, *therefore* male PE < female PE
'unattractive' female= poor parent	positive relationship between crest length and PE, *therefore* male PE > female PE	male PE = female PE

Table 4.2. Predictions of outcomes of parental expenditure (PE) if ornament (crest length) indicates attractiveness (i.e. indirect benefit).

	attractive male	unattractive male
attractive female	male PE = female PE	male PE > female PE (EPF's predicted, in which case male PE < female PE)
unattractive female	male PE < female PE	male PE = female PE (EPF's predicted, in which case male PE < female PE)

and for longer durations and directed more sexual displays to long crested models than to shorter crested models indicating that individuals with longer crests were more attractive to both sexes. Jones and Hunter (1999) found that crest length signalled dominance status in both males and females and concluded that the crest ornament have a function for both sexes and female expression was not a consequence of genetic correlation.

Indirect benefits or the 'good genes' hypothesis, is based on the hypothesis that individuals (males usually) are advertising their genetic quality through elaborate ornamentation or sexual displays (see Andersson 1994 for complete review). Genetic quality may include benefits such as resistance to parasites (e.g. Hamilton and Zuk 1982). While indirect benefits have much more often been the focus of sexual selection studies, they are more "controversial" than preference for displays relating to direct benefits because it is not apparent whether such benefits exist (Johnstone 1995).

Patterns of Mate Retention

Seabirds typically have a high rate of mate retention (see review Choudhury 1995), however crested auklets have a much lower rate of mate retention than most (c. 55% Zubakin 1990; 65% this study). Variation in mate retention in seabirds is often attributed to nest site, age and experience of partner and breeding success (Choudhury 1995). If mutual mate choice is based on crest length, as prior studies have indicated (Jones and Hunter 1993, 1999), a predicted pattern of mate retention would be that both shorter crested males and females should be rejected as mates more often than

mates with longer crests. Another potential outcome of mutual mate choice is the pattern of assortative mating: higher quality individuals should be more selective than lower quality individuals and a positive pattern of assortment can arise from these mating preferences (Burley 1983).

In summary, my study had the following objectives: 1) to investigate how parental effort is related to crest length. I used two different models of mate preferences, one that describes crest length as an advertisement of a direct benefit (level of parental care) and the other that describes crest length as an advertisement of an indirect benefit; and 2) to evaluate whether mate retention is related to crest length or breeding success.

METHODS

Study Species

Crested Auklets are a highly social, colonial seabird in which both males and females invest heavily in their one offspring (Jones 1993a). Mate choice occurs on land and at staging areas by the colony (i.e. on the water) and copulations occur only at sea (Jones 1993b; Hunter and Jones 1999). Incubation, approximately 35 days in length, is shared by both sexes, however the level of contribution by each gender has not been previously quantified. While both sexes participate in the chick rearing process (averaged 35 days; Chapter II), males and females adopted distinct roles early in chick

rearing; males brood more while females provisioned more (Chapter III).

Study Site

I studied crested auklets on Buldir Island (52° 21'N, 175° 56'E) in the Aleutian Islands, Alaska, for three breeding seasons (1996-1998). Buldir, located in the western part of the island chain, provides habitat for one of the largest and most diverse seabird concentrations in the northern hemisphere (Byrd and Day, 1986; Sowls et al., 1978). My study area on Buldir was located at "Main Talus", a colony of an estimated 250,000 Crested Auklets (Byrd et al., 1983; Knudtson and Byrd, 1982).

Measures of Ornamentation

I captured adult auklet pairs at their nesting crevices within the first week after hatching of their chicks. Upon capture, each auklet was fitted with a USFWS stainless steel leg band, sexed using bill shape differences (Jones 1993a) and mass, tarsus and crest length were measured (see Jones et al. 1999 for measurement protocols). All birds (adults and chicks) were measured by GSF. Repeatability (Lessells and Boag 1987; Zar 1996) and measurement error for adults were calculated from birds captured on a study plot.

Ornamentation and Parental Effort

Quantification of parental care was challenging because Crested Auklets nest in rock crevices so visual observations of nest sites were not possible. Therefore, to acquire data on parental activities at nest sites I used radio telemetry. I tagged a total of 21 pairs of crested auklets with transmitters during the three study years (1996: n = 7,

1997: n = 8, 1998: n = 6). Pair members were fitted with a small (3 g) radio attached to their leg band and their activities were logged 24 h per day during chick rearing. Age and pair status sometimes confound results of behaviour with respect to ornamentation (Andersson 1994) and while the age of my study birds was unknown, I attempted to control for pair status by selecting pairs that had been paired the previous year (of the 21 pairs tagged, ten were reunited pairs, nine were pairs of unknown status and two were new pairs [i.e. one previously marked individual with new partner]). All parental activities were quantified in relation to chick age (see Chapter II for breeding chronology and chick aging methodology). I measured provisioning rates (feeds/day) and attendance rates (min/day) throughout the chick rearing period. However, I was unable to standardized parental effort across the entire chick rearing period because transmitter life was variable and males and females differ significantly in their behavior between the early and latter half of chick rearing. Therefore I only examined parental effort during the early part of chick rearing (chick age 1-14) in relationship to ornamentation. Parental effort and pair coordination is particularly critical during this time period as most chick mortality occurs in the first five days after hatching (GSF unpublished data).

To examine whether crest ornamentation could explain the variability in parental effort and whether individuals adjusted their parental effort in relationship to their partner's ornamentation (DAH) I used four step-wise regressions. I used parental effort (one for provisioning and one for attendance), simultaneously with own crest

ornament, partner's crest ornament and partner's parental effort. Males and females were considered separately because of their differences in rates of behaviour in the early part of chick rearing.

Mating and Remating

I followed breeding pairs from 1996 to 1998 to quantify their breeding success and how it related to the likelihood of pairs remating for the following year. Chick growth parameters, hatch date rank, fledging mass and fledging wing; see Chapter II for definitions) were compared between chicks reared by reunited pairs (i.e. same birds paired in previous year) to those reared by new pairs (i.e. one new parent). To examine whether crest length and mate retention were related I compared absolute crest length between reunited pairs and split pairs (i.e. at least one member of a pair mated with new partner in following year) for males and females. Due to the number of birds in my study colony it was not possible to determine whether a bird that disappeared had died or merely moved away. Therefore I used the term 'split' (Rowley 1983) to refer to a pair that did not reunite due either to death of one partner or due to divorce (i.e. active rejection of previous partner).

A possible outcome of a preference for crest is positive assortative mating (Burley 1983). To examine whether Crested Auklets mated assortatively with respect to crest size I used crest length for pairs and applied correlation statistics for all years combined.

Analysis

Crested Auklets have multiple ornaments including auricular plumes, rictal plates, and brightly coloured bill plates (see Jones 1993), therefore it is quite probable that individuals are assessing their prospective mates on the basis of several ornaments (see Møller and Pomiankowski 1993). In my preliminary analyses I included auricular plume length, but in all cases they were non-significant ($P > 0.1$) and were removed them to increase power.

In most of my analyses I used the same data more than once to examine relationships. By doing this I ran the risk of committing a Type I error (Zar 1996). Therefore, in all of my analyses I adjusted the alpha level according to the number of tests conducted using the standard Bonferroni technique (Sokal and Rohlf 1995) and state the number of tests (k) and level of significance in the Results section for each group of tests.

RESULTS

Ornamentation and Condition

Repeatability of crest measurements was high (rI, intra-class correlation coefficient, 0.948; rI SE = 0.02; $F = 2.8$, $n = 19$ $P = 0.1$) and measurement error was low (10.16%). Body size (tarsus) and crest length were positive and significantly related in females, but not in males (females, $r = 0.29$, $n = 59$; $P = 0.03$; males, $r = 0.17$, $n = 59$ $P = 0.21$). Condition (residuals of mass regressed on tarsus, see also Jones et al.

1999) was not related to absolute crest length for males or females (crest: females, r = 0.05, n = 59, P = 0.72; males, r = 0.05,n = 59, P = 0.7).

Ornamentation and Parental Effort

Four step-wise regressions were conducted to investigate the relationships between ornamentation and parental effort. Males' provisioning rates were significantly related to their partner's crest ornament (k = 6, α = 0.008, r = 0.64, F = 4.6, df= 1 and 19, P = 0.002, partner's crest, t = 3.6, P = 0.002; Fig 4.1), while female provisioning was correlated with own crest length (r = 0.48, F = 1.7,df = 1 and 19, P = 0.06; Fig 4.2). Male and female attendance rates were both significantly related to their partner's attendance rates and female attendance was also positively, but not significantly, correlated with her partner's crest length (male: r=0.68, F = 7.9, df = 2 and 18, P = 0.003, partner's crest, t = -1.6, P = 0.1; partner's attendance, t = 3.8, P = 0.001; female: r=0.7, F = 8.4, df = 2 and 18, P = 0.003, partner's crest, t = 1.8, P = 0.08; partner's attendance, t = 3.1, P = 0.006; Figs 4.3 and 4.4).

Mating and Remating

Whether a pair reunited or not was related to only female crest length; females with shorter crests were more likely to split (logistic regression, female crest length: $\bar{x} \pm$ SD, reunited, 43.6 $\pm$ 4.7; split, 37.4 $\pm$ 4.3; F = 7.04, n = 29, P = 0.01; male crest length: $\bar{x} \pm$ SD, reunited 42.8 $\pm$ 6.1; split 43.6 $\pm$ 4.5; F = 0.1, n = 29, P = 0.72). Individuals that split were also more likely to obtain a new mate with a longer crest (Wilcoxon Signed Rank test, crest length: $\bar{x} \pm$ SD, first partner 36.2 $\pm$ 4.1; second

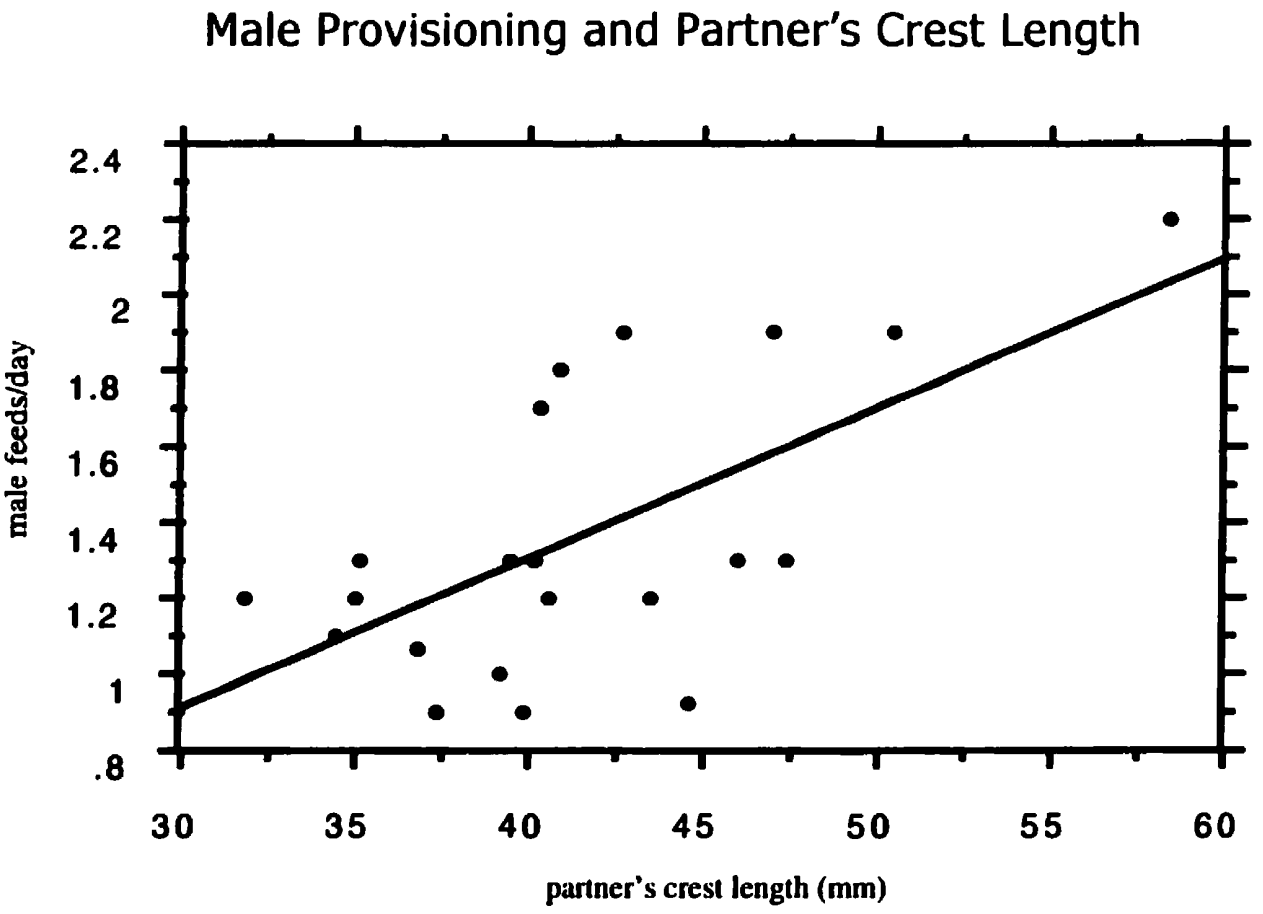

Figure 4.1. Male provisioning and partner's crest length during early chick rearing.

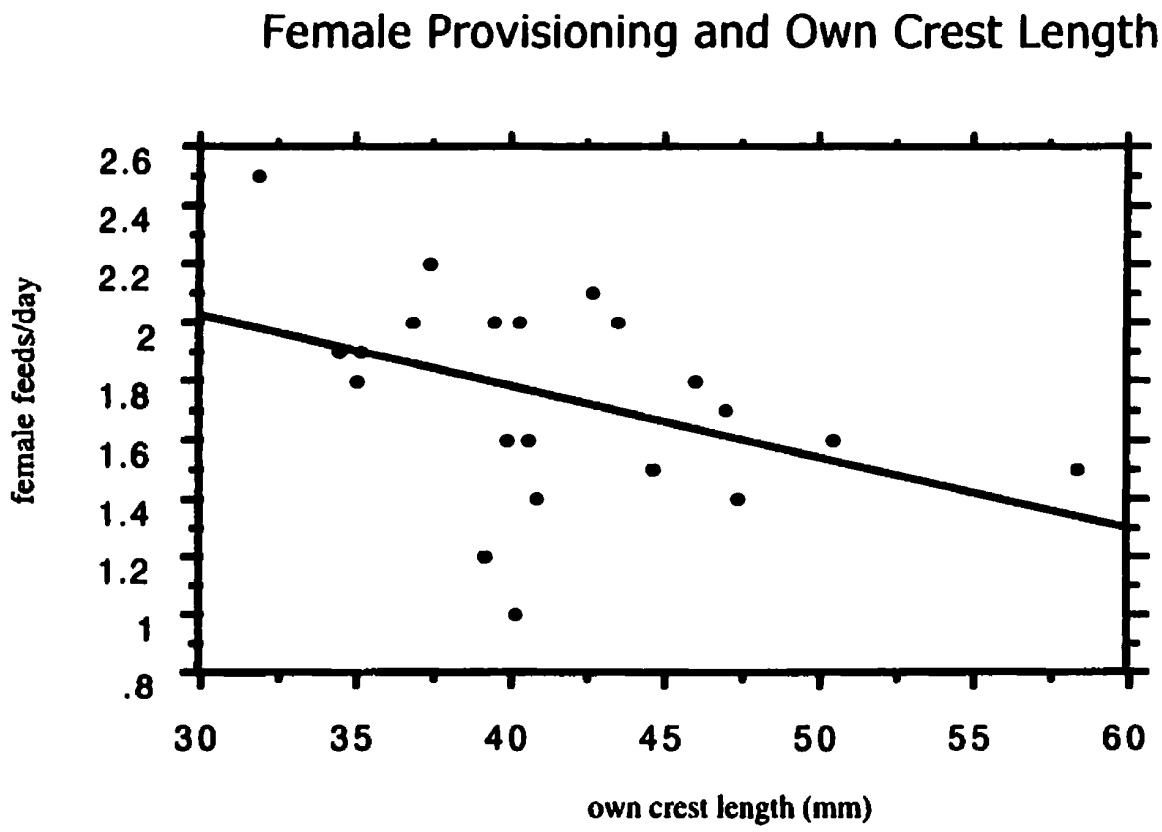

Figure 4.2. Female provisioning and own crest length during early chick rearing.

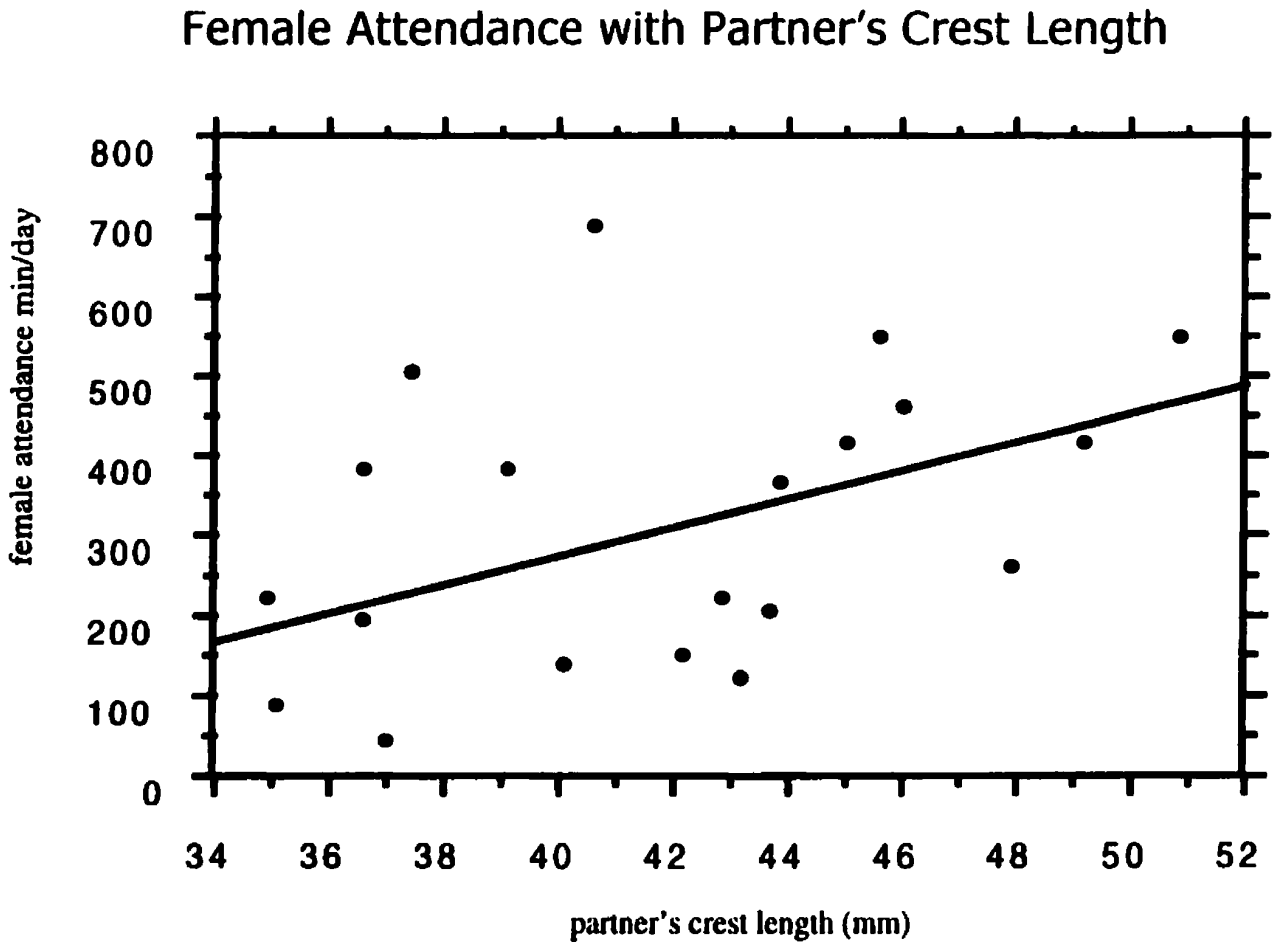

Figure 4.3. Female attendance and partner's crest length during early chick rearing.

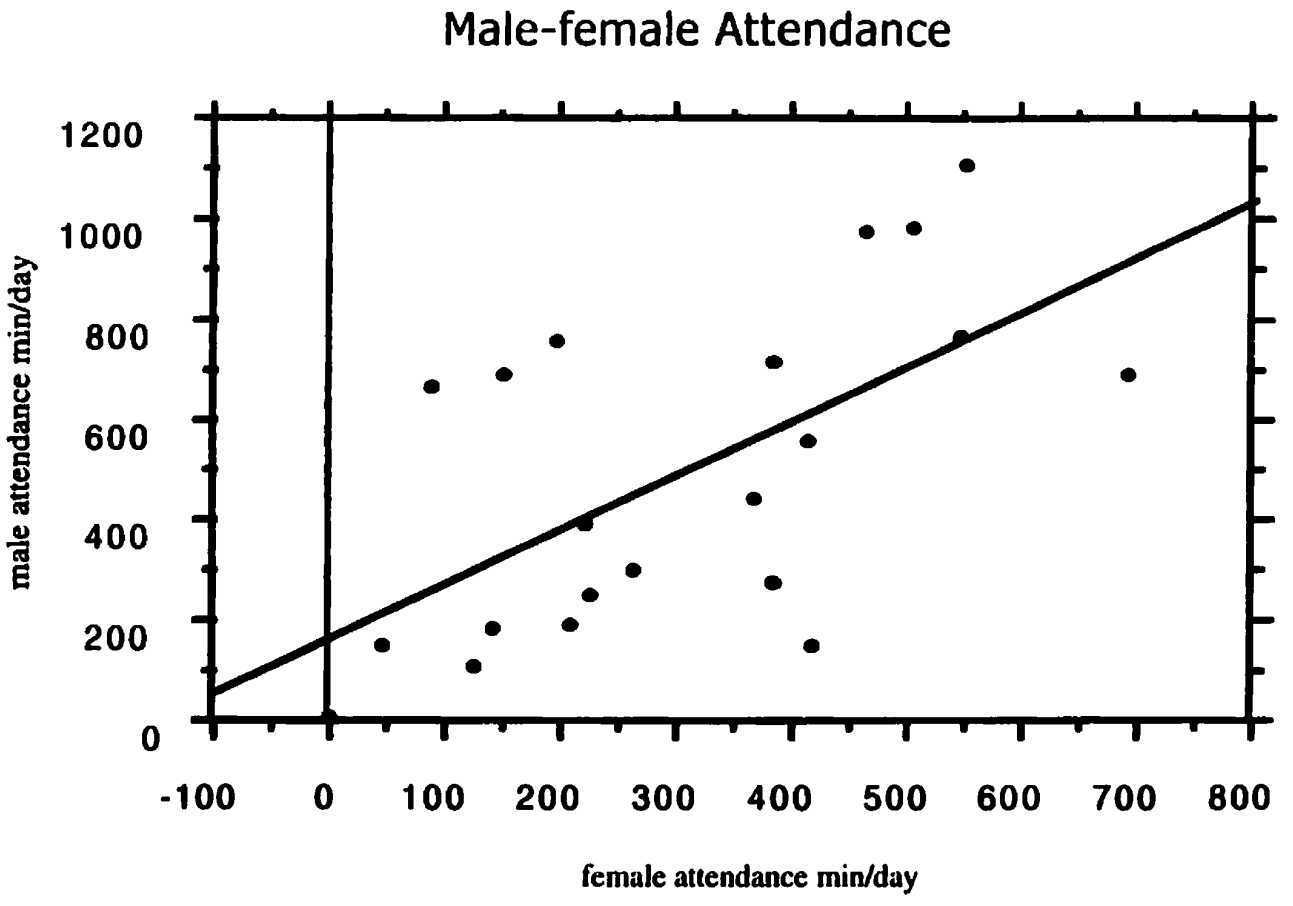

Figure 4.4. The relationship between male and female attendance rates during early chick rearing.

partner 43.8 ± 6.0; z = -2.7, n = 10, P = 0.007). Eighty percent of the individuals that returned to a crevice when a split occurred were males. I found no evidence of assortative mating on the basis of the crest ornament (r = -0.07, P = 0.6).

Crested Auklets on Buldir frequently had a new partner in the following year, though breeding success in one year was not significantly related to whether a pair would reunite or split in the following year (Table 4.3; Fisher exact test, includes only those pairs of which we are certain of the fate, i.e. new pair in crevice or crevice unoccupied not included in test, n = 37, P = 0.2). I examined whether chick growth was affected by pair status (i.e. reunited pairs versus pairs with a new partner) and found that reunited pairs had chicks that hatched earlier than chicks of pairs that split (Mann-Whitney U test; hatch date rank; $\bar{x}$ ± SD, reunited pairs 6.4 ± 7.2; split pairs 9.9 ± 2.4; U = 20.5, n = 25, P = 0.006). Neither fledging mass or wing showed any relationship to remating (Mann-Whitney U test; fledging mass P = 0.9; fledging wing P = 0.8).

DISCUSSION

Crest Ornament as a Direct Benefit

My results indicate that the crest ornament in male and female Crested Auklets was not an advertisement of an individual's ability to provide parental care in the form of provisioning and attendance. In order for this hypothesis to be supported rates of PE

Table 4.3. Patterns of Crested Auklet mate retention and breeding success.

	pair successful	pair failed	comments, possible scenarios
pair successful, same crevice	20	4	certain both alive, no divorce
pair separated	8	5	a. one died; b. divored, one left; c. one skipped a year
new pair in crevice	5	2	a. one died, the other left; b. both died; c. divorced, both left; d. one skipped a year, the other left
crevice unoccupied	7	6	a. one died, the other left; b. both died; c. divorced, both left; d. one skipped a year, the other left

had to be positively related to own crest length, which was not found for either males or females. Furthermore, a result of this positive relationship would be that longer crested males and females invest more when paired with shorter crested individuals, which was also not supported by the data.

Very few studies have demonstrated a relationship between feather ornamentation (an epigamic trait) and paternal care, a direct benefit (Johnstone 1995). Hill (house finches, *Carpodacus mexicanus*, 1991), Sundberg and Larsson (yellowhammer, *Emberiza citrinella*, 1994) and Linville et al. (northern cardinal, *Cardinalis cardinalis*, 1998) found that females who selected brightly coloured males received higher levels of paternal care than females paired with drab males. In all three of these studies male plumage was a condition-dependent trait (Hill 1990). Many more studies have shown a relationship between male courtship behavior (as opposed to an ornament) was reflective of male parental abilities (e.g. courtship feeding rates in common terns, *Sterna hirundo*, Nisbet 1973). However, a demonstration of an ornament advertising direct benefits is not always clear, because females may also obtain indirect benefits such as viability. For example, Alatalo et al. (1991) described a system in which female selection of attractive males in male black grouse (*Tetrao tetrix*) was reflective of male viability (indirect), however a reduced chance of disease transmittance may also influence female choice (direct benefit).

Hoelzer (1989) presented a process in which males can be selected to honestly advertise their parental quality or quantity through an epigamic trait. Although,

Hoelzer did not discuss the possibility of a system in which both males and females honestly advertise parental abilities through an ornament, presumably this could also occur. Mate assessment of parental effort prior to pairing probably exists; however, it may be based on other ornaments or behavior. For example, Crested Auklets engage in courtship displays on the water as well as on land (Hunter and Jones 1999) and mate assessment in of parental abilities may occur on the staging grounds or in feeding flocks or bill color may be a condition-dependent trait that indicates ability to find food.

Crest ornament as an Indirect Benefit

Model #2, in which crest length advertises some indirect benefit, was lent more support by my results because males increased their provisioning rates according to their partner's crest length and longer crested females appeared to provisioned less (negative trend, but non-significant). The case was weaker for females. While I don't have evidence that females did not differentially allocate according to their mate's crest length (positive trend for attendance, but non-significant), but neither did we have firm evidence in support of the hypothesis. To completely support model #2, both males and females should have adjusted their parental effort according to their mates' attractiveness in a system of mutual mate choice based on a crest ornament. Jones et al. (1999) suggested that the crest ornament was an unreliable signal of condition (see also Møller and Pomiankowski 1993), however individuals should not differentially allocate PE according to crest length if it was an unreliable signal. Differential

allocation involves costs which are high enough that individuals should not increase PE unless it may increase their fitness.

Two confounding variables that need to be considered are that females with longer crests are larger (body size) and may be older (and therefore more experienced). I have very little data to explore how crest size changes with age, but there appears to be some indication that it might increase with age (Jones et al. 1999). Older females might be more preferred because of experience; however, from this reasoning I would predict a positive relationship between crest length and PE. Alternatively, age in females may influence laying date or egg size, as was found in another alcid, thick-billed murres (*Uria lomvia*, Hipfner et al. 1997). Female crest length was related to body size (this study; Jones et al. 1999) and larger females may be able to produce a higher quality or larger egg, which would make them valuable as partners.

Mate Retention

While I found no relationship between breeding success and mate retention, it is clear that the benefits of retaining a mate and having an attractive mate were both important in mate choice. Retaining the same mate (and crevice) between years allowed pairs to lay earlier compared with pairs that had switched partners. Choudhury (1995) reported similar mate retention benefits for other species. Also, shorter crested females had a higher likelihood of splitting than did longer crested females and when a split occurred the new mate had a longer crest. So, although there were benefits to retaining a mate, there were also important benefits to obtaining a more attractive partner. Arguably,

since condition related to crest size in females (Jones et al. 1999), it is possible that these shorter crested females had lower survivorship and died instead of being actively rejected by their mate or perhaps short-crested females cannot breed in consecutive years. However, there is no evidence for a difference in male/female survivorship and survival is very high (close to 0.9; Jones and Hunter unpublished data for 1990 to 1998). An association between mate retention and ornamental traits was also found in a closely related species the least auklet (Jones and Montgomerie 1991) in which mate retention was related only to male ornamentation, suggesting that female choice influenced remating.

Conclusions

Møller and Thornhill (1998) concluded that differential allocation to offspring occurs primarily in species where females benefit indirectly from their mate choice and males do not provide extensive parental care. However, contrary to their hypotheses I found that differential investment, occurred in a species in which males contribute substantially in the care of their offspring. I suggest differential investment, based on an advertisement of indirect benefits, may also occur for both males and females, particularly in a species in which both sexes invest substantially in offspring and that has low rates of EPFs (e.g. Hunter et al. 1992). Differential investment may be related to partner attractiveness regardless of their sex.

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SUMMARY

Crested Auklets had chicks that grow relatively fast and depart close to adult size. Chick growth was relatively uniform between colony sites while productivity varied substantially from year to year and between colonies. Male and female adult Crested Auklets had specialized roles in chick rearing and selected different prey types for their chicks, however these behaviours were flexible and sex differences were less apparent in a poor food year (1996). Both male and female Crested Auklets are attracted to longer crested individuals (Jones and Hunter 1993) and while both sexes adjusted their parental effort according to their mate's attractiveness, males had more control over the decision to remate.

Inter-island differences between Crested Auklet colonies were quite distinct and comparisons between Buldir and Kasatochi proved to be valuable because it became apparent that each colony was experiencing different events in the same year. For example, years of higher productivity on Buldir were years of lower productivity on Kasatochi. Kasatochi Crested Auklets appeared to be on a slightly later annual schedule for laying, hatching and fledging than those on Buldir which was probably related to a slight difference in latitude. Social activity at the surface was also later in the day on Kasatochi than it was on Buldir (L. Scharf personal communication) and this difference in timing may indicate that Kasatochi birds were foraging further away from the colony than were Buldir auklets. The productivity differences between the two colonies suggests annual differences in local food availability. Springer et al.

(1996) described Buldir marine avifauna as mainly oceanic and the island's surrounding areas have very little shallow-water habitat with no nearby islands. In contrast, Kasatochi is in the Andreaof Islands cluster with more surrounding shallow-water habitat and thus auklets there may forage more in tidal currents between islands (e.g. Hunt et al. 1993). The U.S. Fish and Wildlife Service is continuing to collect auklet food samples from each island throughout each breeding season which should help us further understand inter-colony differences. However, more detailed knowledge about each islands' local oceanography, zooplankton distributions and important foraging areas would aid greatly in our current understanding of the distributions of auklets in the Aleutians.

Inter-colony and inter-year differences in chick growth appeared to be less variable than productivity and while many of the chick growth variables followed the ups and downs of productivity most of these inter-year differences were not statistically significant. Williams and Croxall (1990) noted that chick fledging mass may not always be a good indicator of food availability for seabirds because in poor food years poor quality chicks die and the high quality chicks survive, while in good food years both are more likely to survive. The fact that 1996 chicks appeared to grow at the same rate as the 1997 or 1998 chicks demonstrated that chick fledging mass was not a good indicator of food availability for Crested Auklets. Breeding success and adult attendance at the colony appeared to be more reflective of a possible food stressed year (Cairns 1987).

Several researchers (e.g. Lack 1968, Perrins 1970, Gaston 1985) have noted that the timing of peak chick nutritional requirements and maximum food availability often coincide for many species of birds, yet mass recession prior to fledging is also a common occurrence. For two of the three study years, Crested Auklet chicks on Buldir did not show large mass recessions prior to fledging, however in 1998 the average mass recession nearly doubled (11%) and corresponded with very late laying dates. So, while there appeared to be some flexibility in laying dates as they pertained to maximum food availability there was also some limitation in how much the breeding season could be extended. It was also curious that Crested Auklets appeared to be the only auklet species that experienced later breeding chronology in 1998 (U.S. Fish and Wildlife Service, unpublished data) and that Kasatochi auklets were not equally late. If the seasonal availability of subarctic marine avifauna is extended for longer periods compared to arctic avifauna than arctic auklet chicks (i.e. St. Lawrence Island) should show more fledging mass recession with the more well defined seasonality and shorter breeding seasons. Shorter breeding seasons could also explain why St. Lawrence Island chicks fledged lighter (Sealy 1968) than chicks on Buldir (Chapter 2). How chick growth parameters change with seasonal changes in abundance of prey still requires further research (Gaston 1985).

Crested Auklets appeared to be highly variable in their response to investigator disturbance and there was a sexual difference to disturbance during incubation. Females were more likely to abandon the crevice after being handled than were males.

The physiological stress of egg laying may cause females to be more sensitive during this time period. Some birds I pulled out of the crevice were attached to my hand (i.e. they were biting me) and one female even stuck her head out of her crevice and cackled at me when I arrived there, while others, did not react well to being handled if they were already stressed. This was particularly evident when I compared the three study years just among the high disturbance group (adults handled) and found adults in 1996 were more likely to abandon, though their breeding success was still comparable to the low disturbance group because of lower productivity that year. The higher abandonment rates in 1996 is yet further evidence that adults were stressed that year. Overall, however Crested Auklets were able to deal with the stress of being handled *after* the chick hatches.

Gowaty (1996) emphasized the need for more studies on female variation in parental care. Seabird studies have taken the lead in this area, probably because female reproductive success is completely dependent upon male assistance in seabirds and therefore parental care investigations usually included data on both sexes. In most species of seabirds studied divisions of labour existed between the two sexes. In Crested Auklets, not only was there variation between males and females in the roles of parental care during chick rearing, but parental effort was also related to the attractiveness of the mating partner.

Male Crested Auklets for two of my three study years brooded significantly more often than did their female counterparts early in the chick rearing period. Male

parental attendance appeared to be required even after the chick attained homeothermic capabilities because of potential attacks from prospecting adults. Morris and Chardine (1990) found that Brown Noody (*Anous stolidus*) chicks were particularly vulnerable to attacks by prospecting adults if the chick was left unattended and they concluded that these attacks may ultimately gain the attacker a nest site and thus enhance their future reproductive success. Since we know that Crested Auklets display some site fidelity between year to year, this could also be the case for Crested Auklets. However, rates of attack or aggressive behaviour may vary according to the level of competition for nest sites and hence may vary among colonies depending on whether the breeding populations at a given colony are expanding or contracting.

Ricklefs (1984) noted that breeding adult seabirds that required chick brooding incurred extra energetic costs. While male Crested Auklets were more aggressive than females and had larger bills which made them better equipped to guard young chicks, they probably also had the capability to go longer without food than females because they were heavier. The physiological fasting that males can withstand was demonstrated by one male's continual stay at his crevice for 72 hours. Mass loss during bouts such as these must be substantial for example, Common Murre research in Newfoundland revealed one loafing male lost 5% of his mass in a 12 hour period (S. Wilhelm, personal communication). Mass loss such as these are probably even higher for Crested Auklets since they are smaller and therefore have a higher metabolic rate. Field metabolic rates of males and females during different activity periods in the

breeding season could help to identify the costs involved in parental care.

While we know sexual differences in parental care behaviour existed at Buldir in years when food was not limited, we do not know whether this is occurring at other colonies. Uttley (1992) demonstrated that breeding Arctic Terns (*Sterna paradisaea*) had significant changes in parental care strategies at colonies with poor food resources. At the colony with no food shortages he found male-female specializations early in chick rearing and concluded that behavioral specializations probably allowed more efficient use of time. Clearly it appears that Crested Auklet parental care was a flexible set of behaviours that varied with food abundance, so it may be very different at other colonies where food is farther away, not as readily available or varies in prey types available. Parental care behaviour should also be different in the presence of terrestrial predators such as foxes or rats that threaten adult lives as well as their chicks. Not only would it be interesting to look at differences in parental care at colonies further north that experience shorter breeding seasons and terrestrial predators, but it would also be good to measure differences in prey types, bill shape and aggression between the sexes at different colonies.

When Trivers (1972) developed the hypothesis that parental care investment is related to the degree of sexual selection it is unlikely that he had the Crested Auklet in mind. However, Crested Auklets provided a unique opportunity in which to investigate the relationships between parental effort and sexual selection. Prior to this study I knew that both male and female Crested Auklets preferred individuals with

longer crests (Jones and Hunter 1993) and from this I predicted that crest length should convey the same information to potential partners for both sexes and that mate retention should also be relatively equal for both males and females. Both males and females adjusted their behaviour according to their mate's attractiveness and it appears that attractiveness is an advertisement of an indirect benefit. Mate retention and therefore mate choice for females was also, at least partially, being controlled by males through male possession of the crevice nest site and also because males appeared to be the sex which invested more heavily in parental care and were therefore the choosier of the two.

Fitting these results into the bigger picture of sexual selection is challenging, primarily because the focus of sexual selection and parental care research has been skewed toward polygamous systems or towards monogamous species in which male parental care is not required for female reproductive success (Gowaty 1996). Also, our current theoretical framework is such that we cannot distinguish between different evolutionary pathways for the development of a sexually selected ornament and it is quite possible we may never be able to fully understand the mechanisms involved. Future research needs to be directed at measuring energetic costs of provisioning and attendance, quantifying individuals' activities as related to crevice acquisition prior to and during incubation and modelling of the directional selection gradient (Lande and Arnold 1983; Andersson 1994) on male and female crests, while controlling for age could reveal the strength of selection on the ornament for each sex. Many questions

on Crested Auklet mate choice and parental care are as yet unanswered and we need to direct research towards understanding how crest length is related to such factors as survival and age and how the quality of parental care changes with age.

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